Modelling cannibalism and inter-species predation for the Cape hake species *Merluccius capensis* and *M. paradoxus*

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Declaration of Authorship

I know the meaning of plagiarism and declare that all of the work in the thesis, save for that which is properly acknowledged (including particularly in the Acknowledgements section that follows), is my own. Special mention is made of the model underlying the equations presented in Chapter 4, which was developed by Rademeyer and Butterworth (2014b). I declare that this thesis has not been submitted to this or any other university for a degree, either in the same or different form, apart from the model underlying the equations presented in Chapter 4, an earlier version of which formed part of the PhD thesis of R. Rademeyer in 2012.

Signed by candidate

Signature Removed

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Abstract

The hake fishery is South Africa's most valuable and harvests two morphologically similar species, the shallow-water Cape hake *Merluccius capensis* and the deep-water Cape hake *M. paradoxus*. Since 1948, annual catches have exceeded 50 000 tons and the current total allowable catch (TAC) is about 150 000 tons, a quantity informed by assessments of the hake resource. Current assessments on which management is based use single-stock models that ignore food-web effects. Usually including such interactions in assessments is problematic because of the complexity of food webs. In the case of Cape hake, however, cannibalism and inter-species predation form a very large component of hake mortality and food consumption, thus making a multi-species model not only more feasible but also likely more reliable.

A comprehensive multi-species model incorporating these interactions was last investigated in 1995. Since then, substantially more data have become available, and hake single-species assessments have developed considerably, *inter alia* now including the ability to take careful account of species differentiation. Additionally, with increased computer processing power, more sophisticated modelling can now be attempted than was possible 20 years ago, rendering an update and refinement of the 1995 analyses timeous.

The thesis uses mathematical methods to model hake-on-hake predation and cannibalism in hake populations explicitly by incorporating an additional mortality term to account for these interactions. Information from stomach samples obtained on hake research surveys on predator and prey lengths, as well as on the proportion of hake in the diet of hake predators, is then included when fitting the model to data. Chapter 1 contains a brief introduction to the work. Chapter 2 provides background information on the Cape hake fishery and its management, as well as pertinent information on the biology and diet of the hake (and related fish) from the literature that is relevant to the development of the model constructed in this thesis. Chapter 3 lays out the data available for assessing the Cape hake populations: abundance indices together with catch and catch-at-size data for the standard non-predation model, and hake stomach content data for the years 1999-2013 to inform the predation component of multi-species model developed. Chapter 4 provides the details for the standard hake assessment model used at present to inform management of the stocks. This model forms the basis for the multi-species model developed incorporating predation, which is presented in Chapter 5. The remaining Chapters of the thesis present the results and discussions (Chapter 6), possible future development of this model (Chapter 7) and a brief summary of the main findings of the thesis (Chapter 8).

The hake predation model is able to take hake-on-hake predation and cannibalism into account explicitly and still provide a reasonable fit to the various sources of data available. There are, however, some indications of data conflicts as well as of potential model over-parameterisation, which need to be addressed. When cannibalism and predation are taken into account, the *M. paradoxus* population exhibits a predation release in first half of the 20th century in response to a *M. capensis* predator population reduced by the early fishery. The *M. capensis* population shows an increase in the 1960s that is not evident to the same extent in the non-predation models, suggesting that the *M. capensis* population also experienced a predation release as a result of reduced cannibalism by *M. capensis*. Despite these predation releases, the predation model estimates similar, even slightly higher, extents of depletion for *M. paradoxus*. The chief reason for this is the requirement to reflect the large drop in the ICSEAF CPUE data from the mid-1950s to mid-1970s. Higher predation levels give greater predation release, but show stronger oscillatory behaviour which is unable to also mimic the ICSEAF CPUE decline. This finding is contrary to the hope expressed by some stakeholders in the fishery that this predation release would result in estimates of a substantially less depleted *M. paradoxus* resource. While the predation model still needs to be developed further, it shows good potential as a tool to improve the assessment and management of what is South Africa's most valuable fishery.

Contents

Chapter 1

Introduction

The fishery for hake is South Africa's most valuable and harvests two morphologically similar species, the shallow-water Cape hake *Merluccius capensis* and the deep-water Cape hake *M. paradoxus*. These hake are opportunistic feeders, and the levels of cannibalism and hake-on-hake predation exhibited by the Cape hake populations are unusually high. The current assessments on which management is based use single-stock models that ignore food-web effects, since the inclusion of such (predominantly) predator-prey interactions in assessments is usually problematic because food webs are typically very complex. In the case of Cape hake, however, the cannibalism and inter-species predation form a very large component of hake mortality and food consumption, thus making a multi-species model not only more feasible to develop, but also likely more reliable.

In South Africa, the call for a hake multi-species model has become stronger in recent years as a result of the unease associated with the high extent of depletion currently estimated by the assessment models for *M. paradoxus*. Given that the *M. capensis* population was probably reduced by fishing in the 1950s and 1960s, it seems likely that the *M. paradoxus* population would have undergone at least some degree of predation release following this reduction of one of its major predators. The current single-stock assessment models with their time-invariant natural mortality (Rademeyer 2008b, 2014b), however, are not able to take account of such predator-prey features, and as a result the depletion levels estimated for *M. paradoxus* may be more severe than is the case in reality.

The need to describe predation and its impact on exploited hake populations has been realised since the 1980s (Roel and Macpherson 1988). Cannibalism and predation can impact the size and age distribution of populations, mortality rates, the stability of the population dynamics and in some cases act as a regulatory mechanism for the population (Link *et al.* 2012). In a study of the marine community off Patagonia, Koen-Alonso and Yodzis (2005) found that while single- and multi-species models exhibited many similar traits, they also showed different behaviours under different exploitation scenarios. Those authors go on to suggest that assessing this community with a single-species model could result in mismanagement with hazardous impacts on the populations in the community.

Considerations such as the above fall within the scope of the Ecosystem Approach to Fisheries, or EAF, an approach that aims to incorporate ecosystem considerations into the more traditional fisheries management in order to sustain both the marine ecosystem and the economic viability of the fisheries operating in that

ecosystem[1] (Garcia *et al.* 2003). Importantly, EAF is an extension, rather than a replacement, of the existing fisheries management framework (Garcia and Cochrane 2005), and has been implemented in several parts of the world, including Australia and parts of the United States (Collie *et al.* 2014). EAF, however, does not come without its own challenges since greater complexity in a model generally requires more parameters to be estimated. Unless sufficient extra data become available to support this added complexity, estimation variance may increase to an extent that more than offsets any reduction of bias. Hence trade-offs have to be considered between what can be estimated with adequate precision from the data available against the risk of mismanagement resulting from ignoring ecosystem effects. Furthermore, certain concepts such as "ecosystem health" and "ecosystem integrity" have a wide range of meanings and are difficult to translate into objective and quantitative management targets (Larkin 1996, Murawski 2000). Link (2002) adds limited resources in terms of time, money and man-power; together with potential dilution of clear-cut management advice, as well as data availability to the list of common reservations against implementing EAF. However, limitations in the knowledge of how ecosystems function should not prevent the development of EAF, and it is argued that detailed analyses of available data and information, rather than a complete understanding of ecosystem functioning, are the necessary first steps to incorporating ecosystem effects into fisheries assessments (Link 2002, Garcia *et al.* 2003).

While many of the issues that EAF aims to address are common across different fisheries across the world, incorporating ecosystem effects into the stock assessments will likely need to be locally tailored (Koen-Alonso and Yodzis 2005). The Cape hake populations provide a unique assessment opportunity since the hake-on-hake predation seems to contribute to a substantial component of hake mortality rates. Thus a multi-species model for the two Cape hake species, taking hake cannibalism and inter-species predation into account, provides a natural next step in the EAF context for these species. If such a multi-species model is to contribute to the management of hake stocks, it should be able to provide qualitative and even more ideally sound quantitative advice regarding the impacts of different management strategies on the hake stocks (Rademeyer 2012). At the very least, however, it can help to better understand the role that cannibalism and inter-species predation play in regulating the hake populations.

A comprehensive multi-species model incorporating these interactions was last investigated in 1995 (Punt and Butterworth 1995). Since then, substantially more data have become available, and hake single-species assessments have developed considerably, *inter alia* now including the ability to take careful account of species differentiation. Additionally, with increased computer processing power, more sophisticated modelling can now be attempted than was possible 20 years ago, rendering an update and refinement of the 1995 analyses timeous.

This thesis uses mathematical methods to model predation and cannibalism in these Cape hake populations explicitly by incorporating additional mortality terms to account for these interactions. Information from stomach samples obtained during hake research surveys on predator and prey lengths, as well as on the proportion of hake in the diet of hake predators, is then included when fitting the model to data. Specific research questions that this thesis aims to address include:

1. What information do hake stomach content samples provide on the levels of hake-on-hake cannibalism and inter-species predation?
2. Is it possible to incorporate effects of hake-on-hake cannibalism and inter-species predation into the standard single-species hake assessment model?
3. Does the inclusion of such effects appreciably change perceptions of the resource status, in particular of the *M. paradoxus* depletion level?

[1] Ecosystem-based Fisheries Management (EBFM) and Integrated Management (IM) are closely related management concepts to EAF (Garcia *et al.* 2003).

4. What further work needs to take place in order to develop a multi-species hake model that is sufficiently robust to provide reliable management advice?

Future developments of this predation model will aim to incorporate other major sources of mortality such as predation by seals and other predatory fish, and as such the model presented in this thesis serves to demonstrate the ability to take hake-on-hake interactions into account, and builds a foundation for such future developments.

Chapter 2 of this thesis provides background information on the Cape hake fishery and its management, as well as pertinent information on the biology and diet of the hake. The Chapter then proceeds to lay the foundation for the development of a hake predation model, by providing details of previous multi-species hake models that have been developed, as well as information on aspects of fish diet from the literature that are relevant to the development of the model constructed in this thesis.

Chapter 3 lays out the data available for assessing the Cape hake populations. First, the data for the standard hake assessment model are listed: abundance indices, catches and catch-at-size data. Secondly, summaries of the hake stomach content data that are available to inform the predation component of model are presented. Background information on the data sources and the research survey sampling strategies used is also provided.

Chapter 4 provides the details for the standard hake assessment model used at present to inform the management of these populations. This model is not the work of the author of this thesis, but its description has been included since it forms the basis for the hake predation model presented in the thesis. This Chapter furthermore gives the details of the changes that were made to this standard hake assessment model to structure it more suitably for the extensions needed to incorporate hake-on-hake predation and cannibalism.

Chapter 5 presents the details and equations for the predation component of the hake model and the refinements that were necessary to develop what is presented as the base case predation model in this thesis. This Chapter also includes several appendices providing details of analyses that were undertaken external to the model to calculate the diet-related quantities that are of relevance to the predation model.

Chapter 6 contains the presentation, and discussion, of the results from the hake predation model, while Chapter 7 outlines possible future developments of this model. Chapter 8 provides a brief summary of the main findings and conclusions of the thesis.

The software used for the modelling work is AD Model Builder, or ADMB, a powerful statistical package for estimating parameters for nonlinear models (Fournier *et al.* 2012), and all model runs were performed using facilities provided by the University of Cape Town's ICTS High Performance Computing team (http://hpc.uct.ac.za). All graphical output was generated in R (R Core Team 2014).

Specification of predator-prey terminology for this thesis

Throughout this thesis, the term "hake predation model" (or simply "predation model") has been used *in lieu* of "hake cannibalism and inter-species predation model" in the interest of brevity.

Furthermore, in the explanations and discussions presented in this thesis, the two hake species occupy variable roles as predators and as prey. The term "hake predators" is thus ambiguous in that it can be taken to refer to either "predators that are hake" or "predators preying upon hake". For the descriptions and discussions in this thesis, the meaning is taken to be the former interpretation, i.e.:

hake predators	are predators that are hake,
hake prey	are prey that are hake,
M. capensis predators	are *M. capensis* hake that prey upon other (*M. capensis* and *M. paradoxus*) hake,
M. paradoxus predators	are *M. paradoxus* hake that prey upon *M. paradoxus* hake,
M. capensis prey	are *M. capensis* hake that are preyed upon by other (*M. capensis*) hake, and
M. paradoxus prey	are *M. paradoxus* hake that are preyed upon by *M. paradoxus* and *M. capensis* hake.

Where necessary, the terms "the prey of *M. capensis* (or *M. paradoxus*) hake" or "the predators of *M. capensis* (or *M. paradoxus*) hake" will be used to describe the second of the two interpretations mentioned above.

Chapter 2

Assessing the Cape hake stocks - why a multi-species model?

2.1 Introduction: the Cape hake stocks

There are two morphologically similar species of Cape hake: the shallow-water *Merluccius capensis* and the deep-water *M. paradoxus*. *M. paradoxus* was originally considered a sub-species of *M. capensis* and was first recognised as a separate species in the 1960's (Franca 1962). The species-status of the two hakes, however, remained unclear until the late 1980s, when morphological and genetic research validated them as two separate species (Durholtz *et al.* 2015).

The shallow-water *M. capensis* is generally found inshore of *M. paradoxus*, predominantly in depths of less than 400m (Payne *et al.* 1987), while the deep-water *M. paradoxus* is found mainly in depths of 150-800m, but also to 1000m (Durholtz *et al.* 2015). Thus there is an overlap between the two species in the range of 150-400m, with the relative abundance of each species changing with depth (Botha 1985). Since hake tend to move into deeper water as they grow larger (Payne *et al.* 1987), it is primarily large *M. capensis* which co-occurs with smaller *M. paradoxus* in this area of overlap.

Both species are distributed throughout the coastal waters of South Africa; however the deep-water *M. paradoxus* is dominant on the West Coast of South Africa, while the shallow-water *M. capensis* dominates on the Agulhas Bank. Reasons for these differences between the distributions are not clear, but Payne (1995) suggests that the wider continental shelf on the South Coast may provide a more suitable habitat for the shallow-water *M. capensis*, while the deep-water *M. paradoxus* would prefer the gentle continental slope on the West Coast (although factors such as temperature could play a role). The respective distributions of the two species are shown in Figure 2.1.

Both species are harvested commercially and the hake fishery is by far South Africa's most valuable, forming the bulk (53% by value) of the South African fishing industry and employing some 8400 people (Durholtz *et al.* 2015). The 2015 Total Allowable Catch (TAC) was 147 500t. Historically hake were fished almost exclusively by demersal trawling, until the 1990s when hake-directed longline was introduced to the commercial fishing sector (Fairweather *et al.* 2006). The current demersal hake fishery is split into four sectors: offshore trawl fleet (85%

of the total catch), inshore trawl fleet (6% of the total catch), longline fleet (6% of the total catch) and handline fleet (3% of the total catch). More details on these sectors are provided in Chapter 3.

2.1.1 Fisheries and Management

The South African demersal fishery began at the turn of the 19th century and until 1977 operated largely as an open-access fishery. Initially, hake was landed as incidental catch, secondary to the targeted sole (*Austroglossus pectoralis*), and hake catches started to increase only after the First World War (Rademeyer 2012). Catches increased steadily from 1950 to 1972, coupled, however, with a drop in catch-rates (Andrew and Butterworth 1987). Following the introduction of a 200nmi Exclusive Economic Zone in 1977, a conservative stock rebuilding strategy was adopted and TACs were set by the South African authorities, based initially on recommendations made by the International Commission for South East Atlantic Fisheries (ICSEAF) (Rademeyer *et al.* 2008a). ICSEAF divided the coastal waters around Southern Africa into 8 management divisions, of which Divisions 1.6, 2.1 and 2.2 correspond to the current West Coast and South Coast management areas (see Figure 2.2).

Since the 1990s, the hake stocks have been managed under the Management Procedure (MP) approach. In this approach, the harvesting of a resource is managed by setting annual regulations, such as TAC or limits on fishing effort, by the application of a formula. This formula has pre-agreed inputs in terms of resource monitoring data and undergoes rigorous simulation testing before being implemented, so that it has been checked to provide robust performance under a wide range of possible future scenarios (Butterworth 2007). Importantly, it has a feedback mechanism to adjust regulations in response to the information provided by new data as they become available (Butterworth 2007). Apart from reducing the workload that would otherwise be associated with annual assessments (MPs are normally implemented for three to five years), the MP approach allows for formal consideration of uncertainty and informs the choice of decision rules based on their predicted medium-term consequences (Cochrane *et al.* 1998). In South Africa, MPs are customarily referred to as Operational Management Procedures (OMPs) to emphasise that they constitute the rules actually applied in practice as distinct from a more theoretical construct.

In order to implement an MP approach, a set of Operating Models (OMs) needs to be developed. OMs are similar to the assessment models of traditional fisheries management, except that rather than the focus being on the choice of a single best model, the set of OMs aims to cover the full range of alternative plausible scenarios for the underlying dynamics of the resource and thus represents the uncertainty (for example in stock structure, natural mortality, recruitment) as best as possible. These OMs are then projected into the future under different management scenarios (or MPs) (Butterworth 2007). From the available OMs, a Reference Set (RS) is chosen that is considered to include the primary sources of uncertainties in the assessment. Key performance statistics (for example the current biomass level relative to maximum sustainable yield level (MSYL)) are chosen to summarise the results of robustness trials and to best facilitate considerations of the different trade-offs by managers. Such considerations typically include trade-offs between the risk of depleting the resource *versus* improved catch rates *versus* low variability in the annual TAC (Butterworth 2007).

For the South African hake fishery the primary OMP regulatory mechanism consists of setting TACs, which are calculated from species-specific monitoring data, including commercial CPUE indices and indices of abundance from research surveys (Durholtz *et al.* 2015). South Africa is an international leader in implementing the MP approach and manages, amongst others, its three most valuable fisheries using this approach: hake, sardine and anchovy (*Sardinops sagax* and *Engraulis encrasicolus*) and the West Coast rock lobster (*Jasus lalandii*) (Butterworth and Punt 1999, Punt *et al.* 2014).

Before 2010, the South African government branch responsible for managing the fisheries was known as the department of Marine and Coastal Management (MCM). In 2010, the branch was moved from the Department of Environmental Affairs and Tourism (DEAT) to the newly created Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (DAFF) (Rademeyer 2012), which has managed South Africa's fishery since that move. A summary of the management history of the Cape hake fisheries, collated from Rademeyer (2012) and Durholtz *et al.* (2015), is provided in Appendix 2.A.

2.1.2 Status of the Cape hake stocks

Before 2007, the hake OMPs were based on species-aggregated models, since the basic catch and effort statistics collected from the fishery are not species-disaggregated (Rademeyer 2012). In the years leading up to OMP-2007 (the OMP applied for the years 2007 to 2010), species-splitting algorithms for catch and CPUE data were developed, allowing assessments to move from species-aggregated to species-disaggregated. These new assessments, somewhat unexpectedly, estimated very different depletion levels for the two species, with *M. paradoxus* at only about one third (i.e. well below) and *M. capensis* at more than double (i.e. well above) MSYL (Rademeyer *et al.* 2008b). The then most recent previous assessment, which had separated the West and South coasts but aggregated across the two species, had indicated that the West Coast component of the resource had recovered having almost reached MSYL, and that the South Coast component was well above MSYL (Butterworth and Rademeyer 2005 — see Figures 5 and 6 thereof). While no single factor alone accounted for the much more depleted status of *M. paradoxus*, the main reason was probably that the cumulative historical *M. paradoxus* catches had likely been roughly double those of *M. capensis*, with a rapid increase in catches in the 1960's and 1970's (Durholtz *et al.* 2015). Regardless of the underlying reason, this *M. paradoxus* depletion level seemed to be robustly determined and consistent with all the data sources used in the assessment (Rademeyer 2012). This result caused much concern regarding the status of the *M. paradoxus* population, in particular because of its certification with the the Marine Stewardship Council (MSC), which had been awarded in 2004 based on the earlier estimate of depletion for the combined species assessment that had implied a much healthier state for *M. paradoxus*. The primary objective of OMP-2007 thus became to recover the *M. paradoxus* stock to MSYL over 20 years, as well as increasing the catch rates of the offshore trawl fleet by 50% over the next 10 years, as both species had shown a declining trend in the previous decade, likely owing to poor recruitment. A challenging period of TAC reductions followed over the next few years (Rademeyer 2012).

OMP-2011 refined the hake assessment further by introducing gender-disaggregation and estimating gender-specific growth curve parameters in the model through fitting to age-length keys. The gender-disaggregation was deemed necessary given definite differences in growth rates between males and females (Durholtz *et al.* 2015), and the reasons for estimating the growth curve parameters in the model are explained further in the section on hake growth later. The model refinements, in combination with additional survey and CPUE data showing an upward trend, led to the assessments used in the development of OMP-2011 estimating a *M. paradoxus* depletion level in 2009 of 16% relative to pristine spawning biomass, in contrast to the 10% estimated for 2006 in the assessments used in the development of OMP-2007. The 2007 and 2011 OMPs were successfully implemented with the result that the 2012 TAC (144 670t) was almost back at the 2006 level (150 000t) (Durholtz *et al.* 2015).

OMP-2014, which has been adopted and implemented to set TACs for 2015 and 2016 (Rademeyer and Butterworth 2014a), was chosen making use of a Reference Set that covered three main areas of uncertainty. Assessments used in the development of OMP-2011 had already revealed that estimates of the *M. paradoxus*

depletion are particularly sensitive to assumptions regarding how the pre-1978 catches are split between the two species, so that the associated assumptions, along with stock-recruitment curves and natural mortality, were the major focus for evaluating uncertainty in OMP-2014. The assessments used in the selection of OMP-2014 estimate *M. paradoxus* and *M. capensis*, respectively, at 18% and 69% of pristine biomass levels in the year 2013, with *M. paradoxus* now almost at MSYL (Rademeyer and Butterworth 2014a).

2.1.3 Stock structure

Stock structure of the two hake species remains uncertain. There are two main questions: first, whether the West Coast and South Coast component of each species are comprised of one or two stocks (recent evidence suggests a single stock for each species across the West Coast and South Coast of South Africa as the most likely situation, Rademeyer 2012), and secondly whether the Namibian hake resource (which is managed separately from the South African) is comprised of separate or the same stocks.

An extensive review on the South African - Namibian hake stock-structure question was conducted at the 2014 International Stock Assessment Workshop (IWS) based on information available at the time. Prior to this review, several different studies had found varying evidence for both single and multiple stocks for both *M. capensis* and *M. paradoxus* (Burmeister 2005, von der Heyden *et al.* 2007). The 2014 review was based on unpublished genetic data made available to the workshop, as well as information provided by the analyses of the GeoPop model (Kristensen *et al.* 2014) which combines spatio-temporal information with a simple stock dynamics model to estimate how the size- and spatial-distributions of the stocks vary with time. The panel concluded that it was unlikely that there was a hard boundary between South Africa and Namibia, especially given that there was no evidence of spawning of *M. paradoxus* off Namibia. The information presented at the workshop was most consistent with the hypotheses of a single, shared *M. paradoxus* stock, and two *M. capensis* stocks (one northern, one southern, and an area of mixing between the two). It was recommended that these hypotheses be implemented for the initial development of a trans-boundary assessment. It was noted, however, that the genetic information for *M. paradoxus* could also be interpreted as a single stock with multiple sub-stocks that exhibit different migration behaviours, and that *M. capensis* could also comprise three stocks (Namibian, South African West Coast and South African South Coast stocks), and that the stock-structure should be investigated further in the future (full details of the panel recommendations for IWS 2014 can be found in Dunn *et al.* 2014).

Transboundary assessments and management bring their own set of challenges, as trade-offs between the political and logistical complications of joint management on the one hand, and the potential risks that could arise through incorrect assumptions about stock structure on the other, need to be discussed between scientists and managers from the two countries. Joint assessments incorporating the stocks from both countries are in the process of being developed under the direction of the Benguela Current Commission (Durholtz *et al.* 2015).

2.1.4 Overview of aspects of the biology

Information on general taxonomy, anatomy and biology can be found in Botha (1980) and Payne and Punt (1995).

Spawning and maturity

Both species appear to spawn off the western Agulhas Bank throughout the year, but with definite concentration of spawning in certain months. Historically, hake were believed to spawn predominantly between September and April with a peak in November/December, but more recent studies suggest that most spawning occurs between June and October with a peak in August (Botha 1985, Rademeyer *et al.* 2014, Durholtz *et al.* 2015). Singh *et al.* (2011) found that *M. paradoxus* females mature faster (50% reach maturity at 41cm or roughly 3 years) than *M. capensis* females (50% reach maturity at 53cm or roughly 4.5 years). Fish smaller than 16cm in length (younger than one year), for which the gender cannot be determined macroscopically, are considered juvenile (D. Durholtz, *pers. comm.*). Larvae and small (<10cm) juveniles are entirely pelagic (i.e. not in close proximity to the sea bed), and only start "settling" into a demersal life strategy as they approach the age of one year (D. Durholtz, R. Leslie *pers. comm.*).

Growth

M. capensis hake generally grow faster than *M. paradoxus*, and for both species females grow faster than males (Durholtz *et al.* 2015). Females of both species up to the age of 12 have been caught in surveys, but no males older than 9. For *M. paradoxus* this could be due to older males moving to greater depths than where the surveys operate, but the same explanation cannot be offered for *M. capensis* and the absence of older males may be an actual characteristic of the population. Also of interest is that the maximum recorded ages for Cape hake are lower than for hake species elsewhere, suggesting that the Cape hake may experience rather higher mortality than what is assumed normal for other hake species (Durholtz *et al.* 2015).

Growth curve parameters were traditionally estimated from hake otoliths collected on research surveys for input into the hake assessments. Slower-growing younger hake, however, are generally under-represented in these surveys owing to the fishing gear selectivity against smaller fish. Hence, the growth parameters are now estimated directly in the hake assessments by fitting to age-length keys (Rademeyer and Butterworth 2014b, Durholtz *et al.* 2015).

Migration

No concrete evidence of seasonal longshore migration is available for hake populations as a whole. Survey catches do suggest, however, that there is some movement of hake along the coast as they grow, and initial calculations for a hake movement model that estimates these age-specific movement rates have been undertaken (Rademeyer 2015). Since there is little evidence that *M. paradoxus* spawn off Namibia, there has been speculation that the Namibian *M. paradoxus* hake spawn off the West Coast of South Africa and at least some migrate back north (Durholtz *et al.* 2015). Juvenile hake are known migrate vertically to the midwater at night for feeding purposes, as reported in Pillar and Barange (1993, 1995).

2.1.5 Diet and feeding habits of the Cape hake

Hake are well known to be opportunistic feeders, consuming available prey in relation to the prey's abundance in the predator's environment (Payne *et al.* 1987, Roel and Macpherson 1988, Punt *et al.* 1992, Pillar and Barange 1993). This observation is supported by the difference in their summer and winter diets (Payne *et al.* 1987) as well as observations directly linked to prey abundance: for example Pillar and Barange (1993) report that for hake collected at a site dominated by anchovy (*Engraulis capensis*) recruits, the stomachs of these hake contained mostly anchovy. Pillar and Barange (1993) show further that juvenile *M. capensis* exhibit a preference

for large visible prey over smaller and perhaps more abundant prey, but that this preference is dependent on the availability of such large prey types. An important aspect of hake feeding, especially from a modelling point of view, is the assumption that hake consume "single meals", i.e. that they do not eat again until their current meal has been almost completely digested. This assumption is supported by the observation that well digested and fresh food items are not commonly found together in a single hake stomach (Payne *et al.* 1987).

The main prey types of Cape hake are small crustaceans, fish and cephalopods (Roel and Macpherson 1988, Punt *et al.* 1992). Small hake (<25cm) feed predominantly on crustaceans, but become progressively more piscivorous as they grow larger, with small hake forming an important constituent of the diet of larger (>60cm) hake (Pillar and Barange 1993, Punt and Leslie 1995).

Both species of hake are cannibalistic, and inter-species predation is prevalent where the distribution of large *M. capensis* (as predators) overlaps with small *M. paradoxus* (as prey) (Punt and Leslie 1995). *M. paradoxus* is not known to prey on *M. capensis*, and Payne *et al.* (1987) report a ratio of *M. paradoxus* to *M. capensis* prey of 100:0 for *M. paradoxus* predators, and 74:26 for *M. capensis* predators when considering hake-on-hake cannibalism and predation.

While cannibalism is common among piscivorous fish (Link *et al.* 2012), the level at which this occurs in Cape hake is unusually high. Punt and Leslie (1995) estimate that up to 36% of the diet of large *M. capensis* predators consists of hake, while large *M. paradoxus* predators consume up to 56% hake in their diet, proportions which are large compared to situations elsewhere, for example among groundfish in the north east Pacific (A Punt, *pers. comm.*). While cannibalism and predation in themselves will lead to a stable equilibrium or oscillations about one, the extent to which they hamper the recovery of a depleted population (such as *M. paradoxus*), or the extent to which increased or decreased fishing pressure on the predator population would affect the prey population, could be substantial (Link 2002).

Hake is eaten by many organisms. While there are insufficient data for an explicit estimation of the proportion of the total hake mortality that is caused by various predators, the trophic interactions for the southern Benguela have been analysed using various ecosystem models, providing an indication of the impact that each of these predators likely have on hake. Table 2.1 lists some of the information available in the literature; this information suggests that the major predators of hake are hake, seals, snoek, other large pelagic fish (e.g. kob, yellowtail, tuna) and pelagic chondrichthyans. However, Payne *et al.* (1987) point out that since hake is the dominant species in its habitat, the major predator on hake is probably other hake. The Benguela Ecology Programme conducted an investigation into the quantities of different prey fish consumed by different predators off South Africa and Namibia, in order to identify the most important predators of hake in the Benguela ecosystem (Butterworth and Harwood 1991). Their findings are reproduced in Table 2.2. They estimated that on the West Coast of South Africa, roughly 75% of the consumption of hake by major predators is by other hake.

Thus, in summary, given (a) that hake are opportunistic feeders, (b) that hake is the dominant prey species in the habitat of hake predators and likely *vice versa*, and (c) the high reported levels of cannibalism and inter-species predation for Cape hake, these predatory mechanisms are likely to play an important role in regulating the hake population as mortality rates are consequently density-dependent. Given that current hake assessments assume a natural mortality independent of hake predator abundance, taking cannibalism and inter-species predation into account formally in a multi-species model could have substantial impact on the prevailing perception and understanding of the resource.

2.2 Developing a predator-prey model

Plagányi (2004) separates the range of different approaches that can be used to develop multi-species models into two broad categories: whole-ecosystem models that attempt to incorporate all tropic levels in the ecosystem, and Minimum Realistic Models (MRMs, Punt and Butterworth 1995) that restrict the model to species that are likely to have the most consequential interaction with the species under assessment. Over the years, further categorisations of ecosystem models have emerged as (i) conceptual models (understanding ecosystem processes), (ii) models focused on broad scale strategic management decisions and (iii) models for tactical management advice such as TAC and harvest rules (Plagányi *et al.* 2012, Collie *et al.* 2014). Models such as ECOPATH with ECOSIM (EwE) and the individual-based model OSMOSE (Shin *et al.* 2004) fall under the whole-ecosystem or conceptual categories, and while they are useful for developing understanding of ecosystem functioning, care must be taken to account for uncertainties in the input assumptions of these models (Plagányi 2004). The proposed Cape hake predation model constitutes an intermediate step between a single-species and an MRM approach[1].

A multi-species model can be developed through the incorporation of inter- and intra-species interactions into components of a single-species model. Since the juveniles of a population are most affected by cannibalism, many multi-species models incorporate a cannibalism component into the formulation of recruitment (Link *et al.* 2012). Alternatively, these effects can be taken into account through density-dependent mortality rates, which is the approach that has been taken to develop the Cape hake predation model presented in this thesis. A central component of predator-prey models is the functional response that relates the amount of prey consumed to the prey and sometimes predator population density.

2.2.1 Functional response

The term "functional response" has become particularly connected with the work of Holling (Holling 1959b, Holling 1959a), who categorised the relationship between prey density and the rate at which prey is caught into three types. The first, a Holling Type I functional form, is a linear relationship that simply assumes that the prey catch rate is proportional to the prey density. The Holling Type II functional form introduces a "handling time", which represents that time that predator cannot spend searching for further prey owing to the capture and consumption of a prey item. This handling time can also be interpreted in terms of predator saturation or digestion limits — the amount of prey an individual predator is physically able to consume cannot increase indefinitely with prey abundance. The shape of the Type II functional form has a gradient that decreases with increasing prey density until a saturation level of constant prey consumption is eventually reached. The third, a Holling Type III functional form, has a sigmoidal shape, where the gradient of the curve initially increases and later decreases with prey density until a saturation point is reached. A Type III response has been linked to predator learning whereby a predator might become more efficient at hunting a certain prey type with greater exposure to that prey, before eventually reaching saturation (Jeschke *et al.* 2002, Koen-Alonso and Yodzis 2005, Dawes and Souza 2013).

The form of the functional response chosen depends on the understanding of the resource in question. However, in most cases there is not sufficient information to favour any particular form, but the comparison of different functional responses implemented for a given model can provide insight into how they affect model dynamics

[1]To qualify fully as an MRM, the hake predation model would need to take other consequential sources of mortality, such as predation by seals and other predatory fish, into account.

and outputs (Koen-Alonso and Yodzis 2005). Type II is generally the most commonly implemented functional form, but many of the observations come from a laboratory set-up where an individual predator interacts with individual prey; a Type III response is suggested to be not uncommon when a predator interacts with several prey (Jeschke *et al.* 2002, Koen-Alonso and Yodzis 2005). While the three Holling type functional forms are generally the most well-known, there are many other forms which could be implemented, as illustrated by Kinzey and Punt (2009) who test a further four types in their study.

2.3 Cape hake multi-species models

The Cape hake predation model presented in this thesis is not the first such multi-species model to be developed. A substantial analysis was undertaken in the 1990s by Punt (1994), Punt and Leslie (1995), Punt *et al.* (1995), Punt and Butterworth (1995) and Butterworth *et al.* (1995) in developing a Minimal Realistic Model that incorporated hake cannibalism and predation effects, as well as interactions with the Cape fur seal (*Arctocephalus pusillus pusillus*). In the late 2000s, OLRAC (2008) and OLRAC (2011) performed some preliminary assessments that again took hake predation and cannibalism into account. An overview of these two sets of work is provided below.

2.3.1 The Punt (1994) analyses

Punt (1994) is a comprehensive report on the combined work of Punt and Leslie (1995), Punt *et al.* (1995), Punt and Butterworth (1995) and Butterworth *et al.* (1995), pre-dating these publications. Thus the term "Punt (1994) work" refers to an accumulation of all of the above, and unless indicated otherwise the summary provided below has been taken from Punt (1994).

A workshop was held by the Benguela Ecology Programme in 1991 on seal-fishery biological interactions (Butterworth and Harwood 1991). The recovery of the South African fur seal after over-exploitation during the 17th and 18th century was discussed in the context of the impact this recovery might be having on the Cape hake fishery. Following recommendations from this workshop, Punt (1994) set out to construct a model that included hake, seals and "other predatory fish" components, and to use this model to evaluate the effect of hake-consumption by seals on catch levels and catch rates of the hake fishery. A further aim was to investigate the extent to which a potential seal cull might benefit the fishery. While this work was not initiated with hake management *per se* in mind, the model developed nonetheless constituted the first comprehensive work undertaken on Cape hake multi-species modelling. Further, substantial analyses of hake stomach content data (see also Punt and Leslie 1995) provided valuable insights into the diet and feeding habits of Cape hake, providing an update to earlier work on hake diet (Payne *et al.* 1987, Roel and Macpherson 1988).

2.3.1.1 The overall approach

The overall approach consisted of three components (Punt and Butterworth 1995). First, the aim was to construct several different OMs each representing a feasible hypothesis about the hake, seal and other predatory fish interactions. These OMs reflected uncertainty regarding different assumptions for future consumption of hake by seals, different levels of predation and cannibalism by hake, and alternative values for certain parameters of the population dynamics. Secondly a simulation exercise was undertaken, whereby 100 sets of pseudo data

were generated for each OM, projecting forward for a period of 20 years. The $f_{0.2}$ harvesting strategy (the OMP at the time, see Appendix I of Punt and Butterworth 1995) was used to simulate future catches. These data sets represented the extent of uncertainty in the model parameters and possible future observations. Lastly, a select number of performance indices were chosen to summarise the results, so that management would be able to assess the impact that different levels of hake-consumption by the seals would likely have on the hake fishery.

The Punt (1994) model itself was an age-structured Minimal Realistic Model (MRM), taking into account only the species that were considered to have the most important impact on the Cape hake: hake, seals and an "other predatory fish" component. Full model specifications and equations are provided in Punt and Butterworth (1995) for the hake component and in Butterworth *et al.* (1995) for the seal component, but the essence of the model is described below.

The model assumed discrete six month time steps with catches taken at mid-year. Apart from the fishing mortality, two survival rates were estimated for hake, one for each half of the year. These survival rates incorporated mortality due to hake predation, seal predation, "other predatory fish" predation and a basal natural mortality, as well as the respective begin-year and mid-year population sizes. The survival rates were estimated by calculating the proportions of deaths due to hake, seal and "other predatory fish" predation, as well as other residual natural causes. Further noteworthy aspects are that the model ignored sex-structure and assumed that recruitment was related to total spawner biomass through a Beverton-Holt stock-recruitment relationship.

2.3.1.2 The hake predation component

The hake-on-hake feeding relationship was assumed to have a Holling Type II functional form. The daily ration of a hake predator of a given age was fixed on input from estimates taken from analyses of hake stomach content data (Punt and Leslie 1995) and assumed to be time-invariant. This daily ration was then split into a hake and non-hake component using the Holling Type II feeding functional relationship that depended on a saturation parameter and the biomass of hake prey available to the predator. This ration of hake was further broken down into a ration by hake prey age using a predator-prey preference function that specified the preference that a predator of a given age would exhibit for hake prey of different ages.

Once this daily ration had been calculated, the total number of deaths due to hake predation could be calculated by multiplying by the number of hake predators at the beginning of each half of the year, and these deaths were translated into survival rates.

Punt (1994) found that the model structure could at times result in unstable behaviour or large fluctuations of questionable reality when large cohorts of predators wiped out the majority of juvenile hake. He addressed this issue through the addition of a competition term in the functional response that reduced the amount of predation when the predator cohort was large, thus damping down fluctuations in population trajectories.

2.3.1.3 The seal predation component

The seal population was modelled explicitly through a deterministic age- and sex-structured population model. Births were assumed to be directly proportional to the mature female population component through a time-invariant, age-dependent pregnancy rate. The survival rate in the first year of life was assumed to be a function of seal pup density. Survival rates thereafter were fixed on input and assumed to be independent of the hake

prey population abundance (i.e. no prey feedback). Seal harvest or culling sizes are available for the twentieth century, and these were split by the model into male and female catches by age in proportion to the model-predicted numbers of each.

The number of hake deaths due to seal predation was calculated in the same manner as the deaths due to hake predators, utilising the model estimates of seal population size.

2.3.1.4 "Other predatory fish" component

The "other predatory fish" population in the model was not fully age-structured, but divided into an adult and a juvenile component. The juvenile component was subject to a basal natural mortality as well as a mortality due to predation by hake and seals, while the adult component was subject to a natural and a fishing mortality. The model-estimated hake and seal abundances thus fed into the survival rate of juvenile fish that later in turn preyed on the hake. Similar to deaths due to hake and seals, a Holling Type II functional form was assumed between the model-estimated hake and "other predatory fish" populations.

2.3.1.5 The likelihood

The model parameters were estimated by maximising a likelihood that included a component for the fit of the hake biomass trajectory to the CPUE trend series available at the time, and one for the proportion of hake in the diet of hake and seal predators. The model-predicted proportion of hake in the diet of hake was aggregated over hake predators aged 4-7, and a penalty added to the likelihood so that the proportion of hake in the diet ideally should be 0.29 and 0.17 for *M. capensis* and *M. paradoxus* predators, respectively. These proportions corresponded to the averages of the age 4-7 groups from Punt and Leslie (1995).

2.3.1.6 Conclusions

Punt and Butterworth (1995) found that the impact of potential seal culls on the hake catches and catch rates would likely be minimal and could even be detrimental since reduced predation on large *M. capensis* by seals could result in increased predation by *M. capensis* on small *M. paradoxus*. This result was, however, heavily dependent on the assumption made that seal consumption of hake involved the nearer-to-shore *M. capensis* only. The majority of the conclusions and discussion, however, focused on the impact of seal culling on the hake fishery, rather than the hake-on-hake predation aspect, since the former was the primary aim of the work. Punt and Butterworth (1995) do not, for example, report what overall proportion of hake mortality was attributable to hake, to seals, and to other predatory fish.

2.3.2 The OLRAC (2008, 2011) analyses

The OLRAC (2008, 2011) analyses were initiated in response to concern expressed over the high depletion levels estimated for *M. paradoxus* by the hake assessment models used to develop OMP-2007 (Rademeyer *et al.* 2008b), especially in connection with the MSC re-certification of the stock. As explained before, it was postulated that predation release of *M. paradoxus* early in the fishery could be leading single-species models to over-estimate the extent to which this population had been depleted below its pristine level.

OLRAC (2008, 2011) present only a summary of these analyses, but in essence the work aimed to use the existing stock assessment methodology (which was sex- and species-disaggregated and had been developed substantially since the Punt 1994 analyses) and incorporate effects of hake cannibalism and inter-species predation into the natural mortality component of the model. Estimates for daily ration and the proportion of hake in the diet of hake predators were taken from Punt and Leslie (1995) and curves fit to each to extrapolate to ages not covered by the Punt and Leslie (1995) results.

The methodology of OLRAC (2008) involved first calculating the percentage of a predator's diet that consists of hake prey of a given species, age and gender. This was accomplished through the use of a preference function that emulated the predator preference for prey of different categories, and using this function to calculate a preference-weighted biomass for the prey. The percent diet composition for each prey species, age and gender was then derived from the preference-weighted prey biomass through a relationship similar to a Holling Type II functional form. The numbers of hake deaths due to predation were calculated by multiplying these percentage diet compositions by the estimates of daily ration from Punt and Leslie (1995) and then finally by the hake population sizes estimated by the model. Through the implementation of Pope's approximation for the catch equation, the number of deaths due to predation could be directly subtracted in the model from the population size.

OLRAC (2008) explored three different variants of the model: (1) a base case cannibalism model, (2) a cannibalism model that reduced the consumption rates by a factor of three, and (3) a cannibalism model that excluded all predation on hake of age zero. For each variant, a likelihood profile for the *M. paradoxus* depletion level was developed by forcing depletion levels of 0.1, 0.2, ... 0.5. The results of these analyses indicated that the large extent of *M. paradoxus* depletion to 10% estimated by the hake assessment models was statistically less likely than more optimistic levels of depletion by about five log-likelihood points.

When OLRAC (2008) was presented to a demersal working group of the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (DAFF), a point of criticism was that the preference function was not entirely consistent with preference data that had been made available to the 1991 Benguela Ecology Programme workshop on seal-fishery biological interactions. OLRAC (2011) provided an upate to OLRAC (2008), with refinements that included: (1) parameters of the predator-prey preference function were estimated (rather than fixed as in OLRAC 2008) by fitting directly to the aforementioned preference data, and (2) models were also fitted to a "reverse" Holling Type II functional form that allowed the proportion of hake in the diet of hake to increase with decreasing prey population size. Furthermore, rather than providing a likelihood profile for the *M. paradoxus* depletion level as in OLRAC (2008), the maximum likelihood estimates were provided.

Results presented in OLRAC (2011) showed an increase in the 2007 spawning biomass estimates for *M. paradoxus* from 11% of pristine biomass to 28% when predation was taken into account. There was little change in the *M. capensis* depletion level (53% to 51%).

2.4 Paving the way: A summary of quantitative and qualitative information relevant to the Cape hake predation model presented in this thesis

Since the Punt (1994) work, substantially more data have become available, and hake single-species assessments have developed considerably, now including the ability to take careful account of species differentiation. Additionally, with increased computer processing power, more sophisticated modelling can now be attempted than was possible 20 years ago. While nevertheless recognising the exploratory OLRAC (2008, 2011) work, a comprehensive update and refinement of the 1990s analyses is timeous and is the aim of the work presented in this thesis.

The predation model developed in this thesis is based on a sex-aggregated version of the latest hake assessment model (Rademeyer and Butterworth 2014b). It draws on elements of the Punt *et al.* (1995) model for the incorporation of cannibalism and predation, but makes substantial use of methods from a more recent multi-species model (Kinzey and Punt 2009). In order to simplify the development process, the model in its current form does not take predation on hake by seals and other predatory fish into account.

Three aspects of the hake diet are of particular importance for the hake predation model:

(i) daily ration,

(ii) the proportion of hake in the diet of hake predators, and

(iii) the preference that a predator of a given size exhibits for prey of different sizes.

Information on predator-prey preference can be readily obtained from recent hake stomach content samples from research surveys (details of these data are given in Chapter 3). In order to analyse the stomach content data to obtain estimates of quantities such as daily ration and the proportion of the diet that a certain prey type constitutes, estimates of the gastric evacuation rate of the predator need to be known. However, no experiments to determine the gastric evacuation rate are known to have been conducted on Cape hake. This is most likely due to the fact that these hake cannot easily be caught alive in the wild as they tend to evert their stomachs as they are pulled from depth, and further cannot easily be kept in captivity owing to their cannibalistic tendencies (Singh, *pers. comm.*).

As such, the Cape hake predation model relies on information available in the literature for similar demersal species to provide biologically realistic bounds for diet-related quantities. This section provides a summary of quantitative information available either for Cape hake directly, or else for other fish species, that was necessary for calculations or useful in checking biological realism.

2.4.1 Gastric evacuation rate

The length of time a predator takes to digest a prey item will determine when the predator needs to feed again. A predator feeding predominantly on prey that evacuates the stomach quickly will feed more regularly and likely consume greater quantities of that prey. Estimates of gastric evacuation rates are thus important in inferring how much of a predator's diet is composed of a certain prey type (and in the case of the hake predation model, the proportion of the diet that constitutes hake) given the preponderance of that prey type in predator stomach

samples. Gastric evacuation rate is generally assumed to depend on temperature and predator size (Punt and Leslie 1995).

Since hake feed predominantly on fish, crustaceans and cephalopods, differences in evacuation rates between these three prey types are of primary interest, but as mentioned above no direct estimates are available for Cape hake. Notable work on Cape hake (Prénski 1980, Payne *et al.* 1987, Punt *et al.* 1992, Punt and Leslie 1995) base estimates of evacuation time on data provided in Jones (1974) for haddock (*Melanogrammus aeglefinus*), cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) predators.

Table 1 of Prénski (1980) provides a range of evacuation rates (in hours) for fish and crustacean prey in hake predators, derived from the Jones (1974) data. The average of these values gives an estimate of evacuation time for fish prey of 75 hours (3.13 days) and 32 hours (or 1.33 days) for crustacean prey. Payne *et al.* (1987), Punt *et al.* (1992) and Punt and Leslie (1995) argue that cephalopods would take longer than crustacean but shorter than fish prey to digest, with an evacuation time closer to the former, and implement a value 50% greater than the value assumed for crustaceans. Following this line of argument provides an estimate of 48 hours (2.00 days) for cephalopod prey.

The values for evacuation rate provided above are the ones assumed for the work presented in this thesis. It should be noted, however, that there are also alternative ways of determining gastric evacuation rates which are described in the literature. A series of papers (see for example Andersen 2001, Andersen and Beyer 2008, Andersen 2012, Andersen *et al.* submitted) relate gastric evacuation to the square root of the mass of the stomach contents and appear to have applied this method successfully and with good accuracy in many cases. They further develop a two-stage model to deal with the digestion of crustaceans with robust exoskeletons, which would take longer to digest initially until the exoskeleton ruptures (Andersen *et al.* submitted). While there was insufficient time to explore these methods in the analyses presented in this thesis, they are worth investigating in the future in the context of the hake predation model (see Chapter 7 on future work).

2.4.2 Daily ration

Punt and Leslie (1995) present estimates of the daily ration of Cape hake, but since no direct experiments have been conducted for hake to determine gastric evacuation rates there is considerable uncertainty associated with these estimates. Essington *et al.* (2001) propose a method that uses the von Bertalanffy growth function to estimate fish consumption rate from size-at-age data, since the derivation of this growth function is based on bioenergetics. Given the uncertainty surrounding the daily ration of Cape hake, the Essington *et al.* (2001) method was applied to hake size-at-age data to estimate bounds on biologically feasible levels of daily ration (see Appendix 5.C of Chapter 5).

In addition to the above, Table 2.3 provides a range of estimates of daily ration expressed as a percentage of body mass for some gadiformes, taken from the literature. These estimates serve to provide a further reality check for the model outputs of daily ration. Expressing daily ration as a percentage of body mass, rather than in absolute terms, has some advantages, especially if the extent to which the daily ration changes with predator age is not known. There is evidence, however, that daily ration as a percentage of body mass tends to decrease with increasing body size. Durbin *et al.* (1983) report 2.9-3.2% for silver hake $\leq$20cm compared to 0.8-2.2% for silver hake >20cm, while Griffiths *et al.* (2009) found that the daily ration of mackerel tuna (*Euthynnus affinis*) decreased 4.10% to 1.95% for medium to large tuna. While this information is not incorporated directly

into the negative log-likelihood of the predation model, it plays an important role in assessing the preference for different model variants in the model development process (see Chapter 6).

2.4.3 Predator preference

It is generally accepted that the prey selectivity exhibited by a predator is largely dependent on the gape-size of the predator (and thus the size of the prey), availability of the prey and the foraging strategies of the predator (Schmitt and Holbrook 1984, Pillar and Barange 1993). In a comprehensive study of 18 predator species, Scharf *et al.* (2000) found that the range of the size of prey eaten by a predator increased with predator age. Their study further revealed that the minimum and maximum prey sizes consumed by predators differed by predator taxa, with some predators preferring prey of 10-20% of predator size, while others not uncommonly consuming prey greater than 50% of their size. For the Cape hake predation model presented in this thesis, the available hake stomach content data were considered a sufficient and indeed the most appropriate source of information on predator-prey preference for the model (these data are summarised in Chapter 3).

2.5 In conclusion

The levels of cannibalism and hake-on-hake predation exhibited by the Cape hake populations are unusually high and, since the hake species is dominant in its own environment, likely constitute a major component of hake mortality. While additionally taking predation on hake by seals and other predatory fish into account (such as in the Punt 1994 work) would undoubtedly improve the realism of the model, the development of a hake multi-species model that takes hake-on-hake predation and cannibalism into account is nonetheless likely to provide valuable insights into the dynamics of the two hake populations, and how this predation may affect the current perception of the stock, in particular in relation to the *M. paradoxus* depletion level. Such ecosystem aspects are likely to provide important matters to consider in the context of the sustainability and management of the South African hake resource. The chapters that follow provide the details of the data that are available to the standard hake assessment, as well as additional diet data available to inform the predation component, and the methods used to develop the hake predation model.

Table 2.1: Table listing the major hake predators and some estimates from ecosystem models of the percentage of the predators' diets that consist of hake. In the table "S" refers to small and "L" to large.

Prey	Predator	% composition
M. capensis (S)	Large *M. capensis*	10-11% [a, b]
	Seals	10% [b]
	Snoek	2-3% [b]
	Cephalopods	2% [b]
	Large pelagics[2]	1% [b]
	Cetaceans	1% [b]
	Pelagic demersal	<0.5% [b]
	Benthic demersal	<0.5% [b]
	Seabirds	0-4% [b]
M. paradoxus (S)	Large *M. capensis*	10-15% [a, b]
	Large *M. paradoxus*	10-15% [a, b]
	Seals	10% [b]
	Snoek	6-13% [b]
	Cephalopods	8% [b]
	Seabirds	3-13% [b]
	Small *M. capensis*	2% [a, b]
	Pelagic demersal	2% [b]
	Cetaceans	2% [b]
	Benthic demersal	<0.5% [b]
M. capensis (L)	Large *M. capensis*	4% [b]
	Pelagic chondrichthyans	4% [b]
	Large pelagics	3% [b]
	Seals	2% [b]
	Benthic chondrichthyans	1% [b]
M. paradoxus (L)	Pelagic chondrichthyans	5% [b]
	Large *M. paradoxus*	2% [b]
	Seals	2% [b]
	Cetaceans	1% [b]

[a]Smith *et al.* (2015) (Atlantis, Ecopath with Ecosim and OSMOSE models)

[b]Shannon *et al.* (2003) (Ecopath model)

[2]Shannon *et al.* (2003) include kob, yellowtail, geelbek and tuna under the category "other large pelagic fish".

Table 2.2: Reproduction of Table 2 of Butterworth and Harwood (1991), showing estimates of the consumption (in '000 tons) of hake by its major predators. The estimates were obtained from analyses of stomach content data, but were considered to be of a preliminary nature since they were based on small datasets and sometimes questionable assumptions, and are likely to be subject to sizeable bias and imprecision. A "??" indicates that there were no data to estimate the consumption.

Predator	Namibia	West Coast	South Coast
Seals	60	200	30
Cetaceans	8	5	3
Seabirds[3]	20	30	20
Hake[4]	??	1000	??
Squid	??	??	??
Predatory fish	300	90	100

[3]Hake consumed by seabirds is virtually all scavenged from fishing trawls.
[4]The assumption was made that there are equal numbers of *M. capensis* and *M. paradoxus* predators.

Table 2.3: Estimates of the daily ration as a percentage of body weight for a selection of gadiformes, obtained from literature.

Species	Common name	Daily ration	Fish size	Source	Cited in
Merluccius capensis	Cape hake	1.1—4.4%		Punt and Leslie (1995)	
Merluccius paradoxus	Cape hake	0.7—4.1%		Punt and Leslie (1995)	
Merluccius bilinearis	Silver hake	2.9—3.2%	$\leq$ 20cm	Durbin *et al.* (1983)	
		0.8—2.2%	$>$ 20cm	Durbin *et al.* (1983)	
		4.0%	"small fish"	Clay *et al.* (1984)	Waldron (1989)
		0.9—1.3%	21—35cm	Pennington (1981)	Waldron (1989)
		1.3—5.7%	"small fish"	Edwards and Bowman (1979)	Waldron (1989)
		0.5—1.0%	"large fish"	Edwards and Bowman (1979)	Waldron (1989)
		0.6—2.2%		Cohen and Grosslein (1982)	Waldron (1989)
		3.4—4.0%	3—10 years	Vinogradov (1977)	Livingston and Goiney (1984)
Merluccius merluccius	European hake	5.0—5.9%	juvenile	Carpentieri *et al.* (2008)	
Merluccius productus	Pacific whiting	0.7—1.1%	2—8 years	Francis (1982)	Livingston and Goiney (1984)
Gadus morhua	Cod	2.3—5.9%		Bromley (1991)	
		0.9—1.5%	$>$ 30cm	Durbin *et al.* (1983)	
		0.5—5.3%	5—100cm	Daan (1973)	Livingston and Goiney (1984)
		1.9—2.5%	23—40cm	Braaten and Gokstad (1980)	Livingston and Goiney (1984)
		0.9—2.2%	23—35cm	Tyler (1970)	Livingston and Goiney (1984)
		1.1—2.8%	18—94cm	Jones (1978)	Livingston and Goiney (1984)
Melanogrammus aeglefinus	Haddock	1.1—2.8%	18—45cm	Jones (1978)	Livingston and Goiney (1984)
		1.5—2.9%	adults	Cohen and Grosslein (1981)	Livingston and Goiney (1984)
		1.8—3.6%	adults	Edwards and Bowman (1979)	Livingston and Goiney (1984)
		0.3—1.4%	34—42cm	Hislop *et al.* (1978)	Livingston and Goiney (1984)

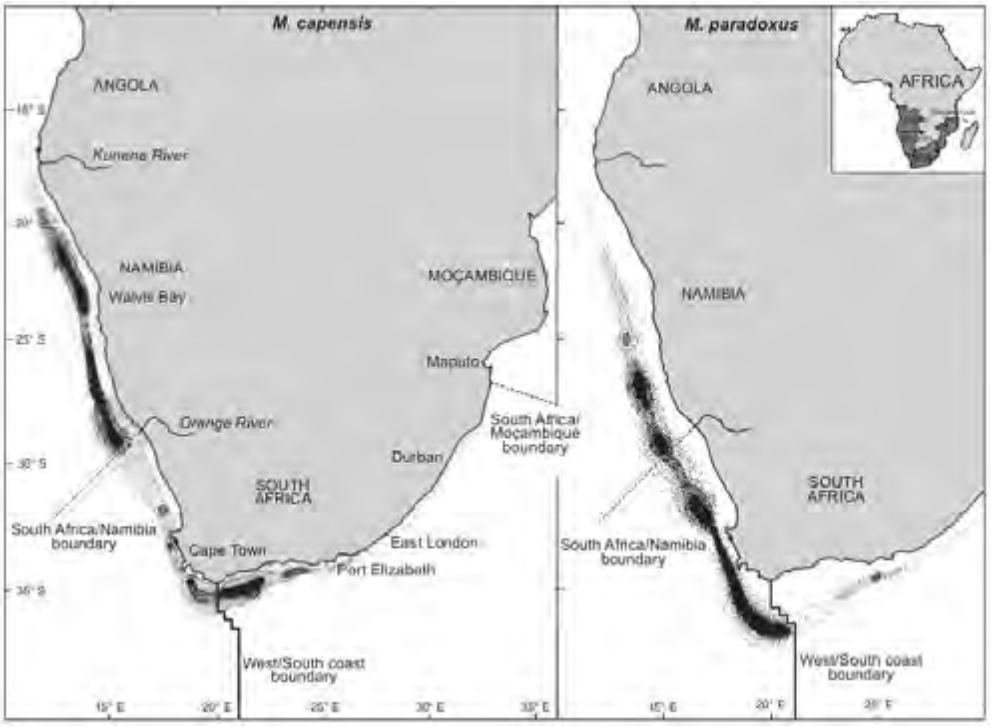

Figure 2.1: The distributions of the *M. capensis* and *M. paradoxus* hake populations (the map has been reproduced from Payne 1995 with permission). Both species are distributed throughout the coastal waters of South Africa; however the deep-water M. paradoxus is dominant on the West Coast of South Africa, while the shallow-water M. capensis dominates on the Agulhas Bank. The West Coast and South Coast boundary is indicated, as well as the management boundary between South Africa and Namibia. The maps were drawn from an analysis of catch positions from catch logs received by the Sea Fisheries Research Institute, as well as some other data sources (A. Payne, *pers. comm.*).

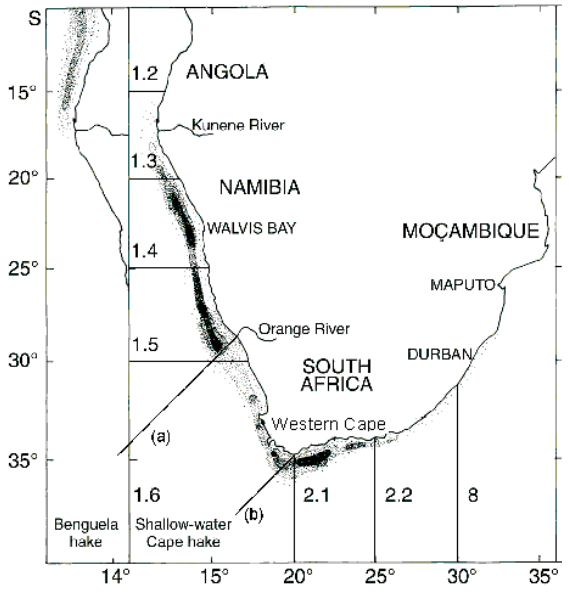

Figure 2.2: A map of the ICSEAF management regions, reproduced from Payne (1995) with permission. The ICSEAF West Coast CPUE series corresponds to division 1.6, and the South Cost CPUE series to regions 2.1 and 2.2.

Appendices

2.A Brief summary of the history of the management of the South African hake fishery, collated from Rademeyer (2012) and Durholtz *et al.* (2015)

Pre-1977	The hake industry off South Africa operates largely as an open-access fishery. Catches start to increase after the First World War, peaking in the early 1970s when they approach 300 thousand tons per year. At some point between 1950 and 1970, the trawl fleet starts fishing in deeper water, shifting its target from *M. capensis* to *M. paradoxus*. Fishing effort from foreign fleets increases dramatically from 1962. Catch rates drop sharply in the 1960s and early 1970s.
1974	Minimum mesh size regulations are introduced for the first time.
1977-1990	South Africa declares a 200nmi Exclusive Economic Zone (EEZ) in 1977. TACs are set by the South African authorities and a conservative stock rebuilding strategy is adopted. TACs are initially based on recommendations made by the International Commission for South East Atlantic Fisheries (ICSEAF) and use of steady-state surplus production models and later on dynamic surplus production models (Butterworth and Andrew 1984).
1990	ICSEAF is disbanded following the independence of Namibia.
1990-present	The hake fishery is managed in terms of the MP approach, except for some transitional periods while the OMP is being revised.
OMP-1991	This OMP provides TAC for years 1991-1996. A species- and age-aggregated dynamic production model linked to a $f_{0.2}$ harvesting strategy is utilised (Punt 1992).
1994	An experimental longline fishery for hake is established. Permanent rights are granted in 1997.
1997-1998	The TAC is held fixed owing to a need to revise OMP-1991 for the following reasons: there was a mis-match in predicted and actual WC commercial CPUE; the need to take account of changes in fishing selectivity over time became apparent; and new GLM techniques for standardising CPUE data needed to be implemented and their results taken into account.
WC-OMP-1999	This OMP is adopted by the Sea Fishery Advisory Council (SFAC) in August 1998 and provides TAC recommendations for the West Coast TAC until 2003. It is based on an $f_{0.075}$ harvesting strategy coupled to an age-aggregated Fox production model (Geromont and Glazer 1998).
SC capensis-OMP-2001	A revised OMP is needed for the South Coast following the development of the longline fishery for hake targeting mainly older *M. capensis*. Since the South Coast *M. capensis* stock was estimated to be well above MSYL, this OMP does not incorporate a stock-rebuildng strategy as for the West Coast, but rather focuses on short to medium term stability in the catch rates.

2002-2006	In 2002, stock trajectories as indicated by an updated assessment fall below the range covered in the simulations of WC-OMP-1999, indicating that the stock dynamics had moved outside the set of scenarios covered by WC-OMP-1999 for which its performance is robust. The TAC is held fixed for a year and then phased down over a period of three years, later extended to four.
2004	The South African hake fishery is certified by the Marine Stewardship Council (MSC), opening new doors to the European market.
OMP-2007	Species-disaggregated assessments are developed, indicating a poor status for *M. paradoxus*. A new coast- and species-combined OMP is adopted as the default basis for TAC recommendations for 2007-2010. The primary objective is to recover *M. paradoxus* to MSYL over 20 years and to increase the CPUE of the offshore trawl fleet by 50% over the next 10 years to enhance economic viability of the fishery. The hake fishery is in a poor condition, with poor recruitment exhibited by both species and declining catch rates for the fishery. A period of challenging TAC reduction follows.
2010	The hake fishery receives its MSC re-certification, with conditions imposed to promote the recovery of the *M. paradoxus* stock.
OMP-2011	The assessment methodology for the hake resource is refined to include gender disaggregation and estimates growth curve parameters directly by fitting to age-length keys. The final choice for OMP-2011 focusses on trade-offs related to future TACs compared to the risk of *M. paradoxus* depletion (together with subsequent recovery).
OMP-2014	The Reference Set of OMs used to develop this OMP is a full cross of factors covering three major areas of uncertainty: three center-years for the species preponderance change in the historic catch, three natural mortality vectors, and three stock-recruitment relationships. *M. paradoxus* is estimated to be at 98% of MSYL. OMP-2014 is used to recommend TACs for 2015 and 2016.

Chapter 3

Hake data

3.1 Introduction

This chapter presents the data available for the hake assessments: the standard data used in the non-predation model (Rademeyer and Butterworth 2014b), as well as additional diet data for the predation model. Some background information to how the data are collected is also provided. It should be noted that the data used to inform the hake predation model correspond to those presented in Rademeyer and Butterworth (2014b), in other words these data extend up to and including 2013. Since then, data for two more years have become available, but these have not been incorporated into the predation model since (a) the update to the Rademeyer and Butterworth (2014b) model has not been comprehensively documented (R. Rademeyer, *pers. comm.*) and (b) validated diet data for the most recent years have not yet been made available.

There are three main sources for data pertaining to the Cape hake (Rademeyer 2012). More details of how these data are incorporated in the assessment are provided in Section 3.2.

1. Annual catch data from before 1955 are obtained from Chalmers (1976).
2. Annual catch data and catch per unit effort (CPUE) data for the years 1955-1977 are available from the International Commission for the South East Atlantic Fisheries (ICSEAF 1989).
3. From 1977 onwards, all data pertaining to hake (catch, abundance indices, catch-at-length data) are provided by the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (DAFF).

As previously mentioned, DAFF is the government department that is responsible for managing South Africa's fisheries. Its primary means of monitoring the hake resource is through information collected on research surveys, as well as from commercial catch data.

3.1.1 Demersal research surveys

Demersal research surveys have been conducted on board the *FRS Africana* since the mid 1980s, with surveys taking place on the West Coast in summer and/or winter (since 1985) and on the South Coast in spring and autumn (since 1986). In 2000 and 2001, owing to technical reasons, the *Africana* was unable to go to sea, and

the *RV Dr Fridtjof Nansen* carried out the West Coast surveys in its place. These surveys are currently not included in the hake analyses since there is no calibration factor available for the difference in fishing selectivities and the catchability of fish between two vessels (Rademeyer 2012). From 2003, new fishing gear was phased in on the *Africana*, for which calibration factors are available and taken into account in the assessments. In recent years, the now more than 30 year old *Africana* has been undergoing extensive repairs and refurbishment, and a commercial trawler, the *MV Andromeda*, has been carrying out the West Coast surveys since 2013 and the South Coast surveys since 2014, with South Coast surveys missed in 2012 and 2013 (D. Durholtz, *pers. comm.*). The Rademeyer and Butterworth (2014b) assessment, as well as the predation model, assume that the fishing selectivity and catchability of fish are the same for the *Africana* and the *Andromeda*, pending a formal evaluation of the calibration factor between the two vessels (Smith *et al.* 2013, DAFF 2014). Recently, Rademeyer and Butterworth (2015) have undertaken some analyses to estimate this calibration factor, but this work has not been taken into account in the predation model at this stage, given that it is only the last year of the model to which this calibration would apply.

3.1.1.1 Survey sampling procedure

The research surveys aim to provide, amongst other information, abundance estimates and population length distributions for various species of interest for monitoring purposes. An overview of the sampling procedure is provided here. Each cruise consists of a series of individual trawls conducted at different stations. The sampling procedure followed for each trawl is as follows (T. Fairweather, R. Leslie and D. Durholz, *pers. comm.*).

1. Generally, all small (<16cm) and large (>40-45cm) fish are sorted by species and measured individually for length.
2. Fish between 16cm and 45cm often form the bulk of the catch and will generally be sub-sampled:
   (a) Since there will be an inclination to pick larger fish first, all the hake are sorted by species and into bins of two size categories: "large" and "small" (these terms are relative within a catch). For some surveys, there are a further two categories for sex, i.e large male, small male, large female, small female. All the bins in each category are weighed individually and noted against the relevant category, but only the total weight is captured in the database.
   (b) Bins are selected at random from the sorted bins to ensure all fish sizes are measured for length. These are referred to as the 'observed' measures. Since larger hake occur less frequently in the catch, in practice this means that generally all bins containing larger hake are measured, and only some of the bins containing smaller hake are measured.
3. Thus for every category of hake in the catch there will be a catch weight (the sum of the weight of all the bins) and a sample or 'observed' weight (the sum of the weight of the bins measured). Note that the fish that are measured individually for length are not weighed individually; only a combined mass is recorded. This is largely because conditions at sea do not allow for a high degree of accuracy when weighing individually.

These samples are used to estimate population densities, abundances, gender- and size-composition of the targeted resources.

3.1.1.2 Biological sampling procedure

A sub-sample of the catch is selected for biological analysis. The primary objective of these samples is to obtain otoliths for the ageing of the fish in order to provide age-length keys, but the stomach contents of the samples are also analysed. In earlier years, the instructions to scientists undertaking the sampling were to collect five specimens per species and length class for biological sampling, collectable across the depth strata. Since smaller hake are encountered more frequently in waters < 300m (owing to the relative abundance and availability to the survey), the focus of biological sampling at greater depths has generally been on larger hake in order to fulfil the sampling target. Since the mid-2000s, the minimum target number of samples required per species and length class has been roughly doubled (and doubled again from about 2010 when approximately 10 samples were collected for both males and females, R. Leslie, *pers. comm.*), and the target per length bin is reset for the second half of the cruise (T. Fairweather, *pers. comm.*)[1].

3.1.1.3 Stratum-density weighting in analyses of survey data

Punt and Leslie (1995) point out that this sampling strategy could lead to biases, in particular when considering predator-prey interactions, since the distribution of predator and prey fish is not uniform and the sampling tends not to be entirely random in order to fulfil the target set for biological samples for each length class. While the resetting of the target for the second half of the cruise will help mitigate this effect, the question still remains whether the biological samples are a reasonable representation of the population as a whole. In light of this concern, an investigation was initiated during the development of the hake predation model to qualitatively assess the extent to which the sampling procedure might bias analyses of the biological data, details of which are provided in Appendix 3.A. Plots of the depth-distributions of the biological samples overlaid with the survey estimated population depth-distributions showed that, for *M. capensis* in particular, a substantial proportion of biological samples were collected at depths for which low population densities were estimated in the surveys. The effect was less marked for *M. paradoxus*, but the conclusion was nevertheless drawn that for the analyses of the biological data, it was more appropriate to weight the samples by the population density of the depth stratum in which they were collected.

Appendix 3.A further investigates the methods in which survey catch-at-length data are analysed. Normally, the assumption is made that the hake population is homogeneously distributed and that all trawls should receive equal weighting. In reality, however, the hake population is not homogeneously distributed, so that it could be argued that the density of the hake population at the location of the trawl should be taken into account when analysing the data. Appendix 3.A provides the details of the methods currently used to calculate catches-at-length, and goes on to provide the equations for calculating catches-at-length taking stratum-density into account. While the differences between the resulting catch-at-length distributions and the impact on the results of the assessment model are minimal, it was considered that the stratum-weighted distributions are less likely to be biased, so that these are the catches-at-length utilised in the analyses of this thesis.

[1] The target sample size for the biological samples is largely a result of processing limitation (in terms of the number of otoliths that can be processed) rather than a formal analysis of variance (D. Durholtz, *pers. comm.*).

3.2 Standard hake assessment data

This section details the data utilised in the standard non-predation Rademeyer and Butterworth (2014b) assessment model.

3.2.1 Annual catches

The commercial fishery does not separate its catch by species, and species identification cannot be made easily from landed and processed catch (Rademeyer 2012). Since the species-disaggregated hake assessment model requires catch-by-species information, the catches are split into species externally to the model. An overview of the splitting procedure is included in the descriptions that follow, with more details to be found in Rademeyer (2012). Table 3.1 provides a list of the annual catches for all the fleets, and Figure 3.1 shows these graphically.

3.2.1.1 Offshore trawl fleet

Deep-sea offshore trawling operates predominantly off the West Coast at depths generally greater than 180m, and on the South Coast restrictions prohibit trawling at depths less than 110m (Rademeyer 2012). More than 80% of the total amount of hake catch is taken by this offshore fleet (Durholtz *et al.* 2015).

The most recent algorithms to split offshore catches taken after 1978 are described in Glazer (2013). These algorithms make use of size-based proportion-by-depth information from research surveys to fit a logistic form to the proportion of *M. capensis* found at various depths. Separate algorithms are used for the West Coast and South Coast, and the respective proportions of *M. capensis* and *M. paradoxus* around the coast are inferred from the size-composition, depth, year and longshore position of data collected on the surveys.

Before 1978, depth information was not recorded for catches, and the algorithms above cannot be used to split the catch. Instead, the annual proportion of *M. capensis* in the catch is assumed to follow a logistic function with time, starting at one in 1917 and decreasing by 1977 to the average 1978-1982 proportion calculated in the algorithms above (Rademeyer 2012). Information available on the historical catches suggests that trawling was initially concentrated in shallower waters around Cape Town and moved into deeper waters over a period centred at some year between 1950 and 1970, and as such the catch would have shifted in that time period from predominantly *M. capensis* to predominantly *M. paradoxus*. The Rademeyer and Butterworth (2014b) assessment model tests various assumptions for the central year when this transition is assumed to have occurred, but the hake predation model implements only their reference case assumption, which assumes 1958 as the central year.

3.2.1.2 Inshore trawl fleet

The inshore trawl fleet operates mainly from Mossel Bay and Port Elizabeth on the South Coast and catches very few *M. paradoxus* since it operates chiefly in depths less than 110m. For the assessment model, catches taken by this sector are thus assumed to consist entirely of *M. capensis*.

3.2.1.3 Longline fleet

The longline fishery developed in the late 1980s and 1990s and operates around the entire coast. Recent species-splitting information has resulted in these catches being made available by DAFF for the West Coast and South Coast for both *M. capensis* and *M. paradoxus*.

3.2.1.4 Handline fleet

The commercial handline fishery started in the late 1980s and operates mainly from Plettenberg Bay on the South Coast at depths of about 100m. Similar to the inshore and South Coast longline fisheries, the handline fishery catches *M. capensis* almost exclusively, and the assessment model similarly assumes that the catches recorded for this sector consist entirely of *M. capensis*.

3.2.2 Biomass indices

There are six series of commercial abundance indices, based on CPUE data, available for assessing the South African hake resource: a historical CPUE series developed by ICSEAF for each of the West and South coasts (ICSEAF 1989) and a GLM-standardised CPUE series for each species and each coast (Glazer 2013). Similar to the pre-1978 offshore catches, the historical CPUE series cannot be disaggregated by species since there is no depth information available from which to allocate catches to the deep-water or shallow-water species. The recent CPUE series have been split by species using the same Glazer (2013) algorithms. These CPUE series are listed in Table 3.2.

Biomass indices are also available from the South Coast spring/autumn and West Coast winter/summer research surveys, which provide fully species-specific information. The biomass estimates and sampling standard errors are listed in Tables 3.3a and 3.3b. The West Coast biomass estimates from 2000 and 2001 have not been included, since the calibration factors between the *Nansen* (the vessel conducting the surveys at the time) and the *Africana* are not known. Calibration factors have been calculated to relate the biomass estiamtes for the surveys that used old gear to those using new gear, and their values are reported in Chapter 4.

3.2.3 Catches-at-length

Species-disaggregated catch-at-length data are available from research surveys and provided in Tables 3.4a to 3.4h, with corresponding plots of the distributions in Figure 3.2. These proportions have been calculated taking the population-density of the depth stratum in which the samples were collected into account, as per the "Sen 2" method of Appendix 3.A. Commercial catch-at-length data cannot be disaggregated by species, because they are often based on processed landed catch. Catches-at-length for the offshore and longline fleets (species-aggregated on the West Coast and assumed *M. capensis* on the South Coast) and for the inshore fleet (South Coast, assumed to be *M. capensis* only) are provided in Table 3.5a to 3.5e, with corresponding plots of the distributions in Figure 3.3.

3.3 Hake diet data

Stomach content data from survey biological samples have been made available by DAFF (T. Fairweather, *pers. comm.*).

- Fully validated[2] biological and stomach content data for 1999-2013 for the West Coast.
- Mostly validated biological and stomach content data for 1999-2009 for the South Coast.
- Mostly validated biological and stomach content data for 2010-2013 for South Coast (actually only two surveys were completed during this period, in 2010 and 2011).

For each stomach sample, information including predator species, length, wet weight, gender and maturity (amongst other attributes) are recorded along with date, depth and geographic location of the catch. Information is also recorded for the stomach contents in terms of the species, number, length and weight of prey items, as well as the state of digestion of these prey items. The overall state of the predator's stomach is also recorded, in terms of various degrees of fullness, or as empty, or everted.

A stomach is classified as everted when the contents are expelled into the mouth by the fish while being hauled from depth, likely owing to a combination of shock, pressure change and temperature change (Payne *et al.* 1987). Tables 3.6a and 3.6b provide a break down of the stomach states of the biological samples by predator species and length class for the West Coast and South Coast respectively. Payne *et al.* (1987) found that larger fish are more likely to evert their stomachs than smaller fish, and also that *M. paradoxus* is more prone to stomach eversion; both trends are evident in the 1999-2013 biological samples. Note that everted stomach samples were excluded from all analyses presented in this thesis.

Table 3.7 provides a summary of the different prey species found in the stomachs of hake predators. A particular point of importance when making inferences from these data regarding overall diet composition is the evacuation rates of the different prey types (see later sections), and to aid analyses the prey items were classified into three main groups: fish, crustaceans (mainly hardened body parts) and molluscs (mainly softer body parts). Tables 3.8a and 3.8b provide a break-down of the prey items into these three groups, by predator species and length group. The trends in these Tables are consistent with other studies (Pillar and Barange 1993, Punt *et al.* 1992), showing that hake become increasingly piscivorous as they grow larger.

Three diet-related quantities are of particular importance for the hake predation model: the daily ration, the proportion of hake in the diet of hake predators, and the (relative) preference a hake predator of given length exhibits for hake prey in relation to their length.

Daily ration

The approaches used to obtain information about the daily ration are summarised in Chapter 2 and Appendix 5.C of Chapter 5.

[2]The data are captured and validated at sea, however several errors were found in the dataset (for example fish number and stomach contents that were swapped, incorrect otolith numbers, hake with "empty" stomachs that had recorded prey items). Furthermore, in the process of correcting the data, errors crept into the excel sheets and some stomach contents were duplicated. The validation process involved checking entries against original log books and also performing various "logical" checks on the data to correct the inconsistencies (T. Fairweather, *pers. comm.*).

Proportion of hake in the diet

In order to calculate the proportion of hake in the diet of hake predators, a fairly complicated procedure needs to be followed to first estimate the mass-at-ingestion of each (partially digested) prey-item, and then to estimate the composition this prey type is likely to have in the overall diet given estimates of evacuation rates for each prey type. Given the subtantial analyses involved in obtaining these proportions of hake in the diet, the resulting proportions have not been included in this data chapter, but are listed in Appendix 5.B of Chapter 5, along with the full details of the analyses.

Predator-prey preference

Data informing the preference that a hake predator of a given size exhibits for a hake prey as a function of the length of the prey have have been obtained from the 1999-2013 DAFF biological data set, in the form of counts of prey items by species and length in the stomachs of predators by species and length. These have been converted to counts by predator and prey ages by calculating the expected age from the von Bertalanffy growth curve. The data for the West Coast are given in Table 3.9. For *M. capensis* predators, hake prey items that have not been identified as *M. capensis* or *M. paradoxus* are not included in the preference counts. Since there is no reason to expect that this failure to identify is correlated with prey species or length, this exclusion is not expected to introduce any bias. For *M. paradoxus* predators, all hake prey are assumed to be *M. paradoxus*. The preference data have not been weighted by depth stratum density, under the assumption that a hake predator's inherent preference for prey of different sizes is unlikely to change with depth.

3.3.1 Coastal segregation

Following a recommendation by the international review panel at the 2014 International Stock Assessment Workshop (Dunn *et al.* 2014), only diet data from the West Coast have been used in the analyses presented in this thesis, since the predation model is not coast-disaggregated[3] and most of the hake population is to be found on the West Coast. The predation model in its current form thus assumes that the diet data from the West Coast applies to the hake populations on both the West and South coasts.

[3] Coast-specific catch, catch-at-length and trend data are incorporated into the coast-aggregated model through an areas-as-fleets approach (see Sections 4.2.9 and 4.2.10).

Table 3.1: The total species-disaggregated commercial catches (in thousand tons) are shown for each fishing fleet for the period 1917-1977. These catches are the same as were used for the Rademeyer and Butterworth (2014b) reference case, which assumes that the central year in the shift of focus of the fishery from *M. capensis* to *M. paradoxus* is 1958 for the offshore catches. West Coast has been abbreviated as WC and South Coast as SC. These catches are illustrated in Figure 3.1.

Year	*M. paradoxus*				*M. capensis*					
	Offshore		Longline		Offshore		Inshore	Longline		Handline
	WC	SC	WC	SC	WC	SC	SC	WC	SC	SC
1917	-	-	-	-	1.000	-	-	-	-	-
1918	-	-	-	-	1.100	-	-	-	-	-
1919	-	-	-	-	1.900	-	-	-	-	-
1920	-	-	-	-	-	-	-	-	-	-
1921	-	-	-	-	1.300	-	-	-	-	-
1922	-	-	-	-	1.000	-	-	-	-	-
1923	-	-	-	-	2.500	-	-	-	-	-
1924	-	-	-	-	1.500	-	-	-	-	-
1925	-	-	-	-	1.900	-	-	-	-	-
1926	-	-	-	-	1.400	-	-	-	-	-
1927	-	-	-	-	0.800	-	-	-	-	-
1928	-	-	-	-	2.600	-	-	-	-	-
1929	-	-	-	-	3.800	-	-	-	-	-
1930	-	-	-	-	4.400	-	-	-	-	-
1931	-	-	-	-	2.800	-	-	-	-	-
1932	-	-	-	-	14.300	-	-	-	-	-
1933	-	-	-	-	11.100	-	-	-	-	-
1934	-	-	-	-	13.800	-	-	-	-	-
1935	-	-	-	-	15.000	-	-	-	-	-
1936	-	-	-	-	17.700	-	-	-	-	-
1937	-	-	-	-	20.200	-	-	-	-	-
1938	-	-	-	-	21.100	-	-	-	-	-
1939	-	-	-	-	20.000	-	-	-	-	-
1940	-	-	-	-	28.600	-	-	-	-	-
1941	-	-	-	-	30.600	-	-	-	-	-
1942	0.001	-	-	-	34.499	-	-	-	-	-
1943	0.001	-	-	-	37.899	-	-	-	-	-
1944	0.002	-	-	-	34.098	-	-	-	-	-
1945	0.004	-	-	-	29.196	-	-	-	-	-
1946	0.011	-	-	-	40.389	-	-	-	-	-
1947	0.021	-	-	-	41.379	-	-	-	-	-
1948	0.059	-	-	-	58.741	-	-	-	-	-
1949	0.113	-	-	-	57.287	-	-	-	-	-
1950	0.275	-	-	-	71.725	-	-	-	-	-
1951	0.662	-	-	-	88.838	-	-	-	-	-
1952	1.268	-	-	-	87.532	-	-	-	-	-
1953	2.558	-	-	-	90.942	-	-	-	-	-

Continued on next page ...

Table 3.1: *... continued from previous page*

Year	*M. paradoxus*				*M. capensis*					
	Offshore		Longline		Offshore		Inshore	Longline		Handline
	WC	SC	WC	SC	WC	SC	SC	WC	SC	SC
1954	5.438	-	-	-	99.962	-	-	-	-	-
1955	10.924	-	-	-	104.476	-	-	-	-	-
1956	19.581	-	-	-	98.619	-	-	-	-	-
1957	34.052	-	-	-	92.348	-	-	-	-	-
1958	51.895	-	-	-	78.805	-	-	-	-	-
1959	76.609	-	-	-	69.391	-	-	-	-	-
1960	100.490	-	-	-	59.410	-	1.000	-	-	-
1961	104.009	-	-	-	44.691	-	1.308	-	-	-
1962	109.596	-	-	-	38.004	-	1.615	-	-	-
1963	129.966	-	-	-	39.534	-	1.923	-	-	-
1964	126.567	-	-	-	35.733	-	2.231	-	-	-
1965	159.704	-	-	-	43.296	-	2.538	-	-	-
1966	154.109	-	-	-	40.891	-	2.846	-	-	-
1967	139.973	7.086	-	-	36.727	7.100	3.154	-	-	-
1968	113.890	13.958	-	-	29.710	13.950	3.462	-	-	-
1969	131.023	18.982	-	-	34.077	18.948	3.769	-	-	-
1970	113.124	11.876	-	-	29.376	11.847	4.077	-	-	-
1971	160.384	15.078	-	-	41.616	15.037	4.385	-	-	-
1972	193.694	23.382	-	-	50.239	23.314	4.692	-	-	-
1973	125.292	36.232	-	-	32.490	36.124	5.000	-	-	-
1974	97.674	45.496	-	-	25.326	45.357	10.056	-	-	-
1975	71.165	33.783	-	-	18.452	33.680	6.372	-	-	-
1976	114.268	26.005	-	-	29.626	25.925	5.740	-	-	-
1977	81.260	18.515	-	-	21.068	18.457	3.500	-	-	-
1978	107.701	4.937	-	-	19.812	2.648	4.931	-	-	-
1979	101.890	3.575	-	-	31.633	3.345	6.093	-	-	-
1980	105.483	3.676	-	-	28.045	2.784	9.121	-	-	-
1981	95.330	1.767	-	-	25.601	3.719	9.400	-	-	-
1982	88.933	5.057	-	-	24.417	6.300	8.089	-	-	-
1983	74.173	7.034	0.126	-	20.260	5.482	7.672	0.104	-	-
1984	86.045	5.718	0.200	0.005	25.210	5.217	9.035	0.166	0.011	-
1985	98.283	12.694	0.638	0.091	26.788	7.322	9.203	0.529	0.201	0.065
1986	107.907	11.539	0.753	0.094	25.898	4.427	8.724	0.625	0.208	0.084
1987	96.162	10.536	1.952	0.110	21.363	5.148	8.607	1.619	0.243	0.096
1988	83.606	8.664	2.833	0.103	22.976	5.852	8.417	2.350	0.228	0.071
1989	85.298	9.039	0.158	0.010	21.961	9.873	10.038	0.132	0.022	0.137
1990	84.969	13.622	0.211	-	18.668	9.169	10.012	0.175	-	0.348
1991	89.371	15.955	-	0.932	17.079	6.119	8.206	-	2.068	1.270
1992	86.777	22.368	-	0.466	16.510	4.094	9.252	-	1.034	1.099
1993	105.114	12.472	-	-	12.951	1.789	8.870	-	-	0.278
1994	106.287	8.588	0.882	0.194	17.580	2.464	9.569	0.732	0.432	0.449
1995	102.877	5.395	0.523	0.202	18.020	1.755	10.630	0.434	0.448	0.756

Continued on next page ...

Table 3.1: *... continued from previous page*

Year	*M. paradoxus*				*M. capensis*					
	Offshore		Longline		Offshore		Inshore	Longline		Handline
	WC	SC	WC	SC	WC	SC	SC	WC	SC	SC
1996	110.460	11.080	1.308	0.568	18.715	2.209	11.062	1.086	1.260	1.515
1997	103.035	13.651	1.410	0.582	14.119	2.185	8.834	1.170	1.290	1.404
1998	113.083	11.703	0.505	0.457	14.570	2.450	8.283	0.419	1.014	1.738
1999	89.147	13.435	1.532	1.288	14.614	1.912	8.595	1.272	2.856	2.749
2000	97.417	9.920	2.706	3.105	20.285	3.610	10.906	2.000	1.977	5.500
2001	101.990	11.016	2.045	0.370	15.606	5.141	11.836	1.750	1.347	7.300
2002	91.720	15.445	4.469	1.585	13.211	3.140	9.581	2.391	2.546	3.500
2003	95.143	21.107	3.305	1.252	10.233	3.926	9.883	2.526	3.078	3.000
2004	86.916	30.746	2.855	1.196	11.315	4.024	10.004	2.297	2.731	1.600
2005	87.540	25.051	3.091	0.472	7.727	4.195	7.881	2.773	3.270	0.700
2006	83.840	22.133	3.241	0.485	9.657	2.494	5.524	2.520	3.227	0.400
2007	96.332	15.825	2.512	3.021	12.537	1.420	6.350	2.522	2.522	0.400
2008	88.290	14.940	2.255	0.809	11.085	2.567	5.496	1.937	1.893	0.231
2009	69.716	13.269	2.410	1.069	10.783	2.431	5.639	2.828	2.520	0.265
2010	70.156	17.863	2.045	0.370	9.738	1.649	5.472	1.750	1.347	0.275
2011	76.744	20.447	3.261	0.905	15.505	1.543	6.013	2.705	2.009	0.185
2012	82.531	19.204	3.582	0.573	11.978	1.751	3.223	2.972	1.272	0.008
2013*	101.350	23.583	4.399	0.704	14.709	2.151	3.958	3.650	1.562	0.010

*Note that the 2013 catches correspond to the TACs set for that year, rather than the actual catches taken, and were used in the predation model in order to be identical to catches assumed for the Rademeyer and Butterworth (2014b) model.

Table 3.2: The values of the CPUE series available to the hake assessments are listed: the species-aggregated historical ICSEAF series for the West Coast (WC) and South Coast (SC) (ICSEAF 1989), and the GLM-standardised series for each species and coast (Glazer 2013).

ICSEAF CPUE (tons/hour)			GLM CPUE (kg/min)				
Species combined			*M. paradoxus*		*M. capensis*		
Year	WC*	SC*	Year	WC	SC	WC	SC
1955	17.31	-	1978	0.74	4.20	1.68	1.09
1956	15.64	-	1979	1.21	4.16	1.84	1.08
1957	16.47	-	1980	1.08	3.86	2.07	1.59
1958	16.26	-	1981	1.11	3.85	2.01	1.03
1959	16.26	-	1982	0.95	3.79	1.99	1.31
1960	17.31	-	1983	1.28	4.08	2.46	1.43
1961	12.09	-	1984	1.35	4.17	2.84	1.55
1962	14.18	-	1985	1.49	4.88	3.45	2.24
1963	13.97	-	1986	1.22	4.25	2.87	2.18
1964	14.60	-	1987	1.07	3.50	2.63	1.94
1965	10.84	-	1988	0.96	3.46	2.79	1.60
1966	10.63	-	1989	1.03	3.74	3.00	1.57
1967	10.01	-	1990	0.87	4.02	3.59	2.34
1968	10.01	-	1991	1.08	4.37	3.24	2.32
1969	8.62	1.28	1992	1.32	3.81	2.96	2.72
1970	7.23	1.22	1993	1.24	3.89	2.13	2.25
1971	7.09	1.14	1994	1.58	4.16	2.88	1.81
1972	4.90	0.64	1995	1.63	3.63	2.71	1.39
1973	4.97	0.56	1996	1.89	3.94	2.50	1.99
1974	4.65	0.54	1997	1.64	3.52	1.82	2.28
1975	4.66	0.37	1998	1.87	3.93	2.09	1.93
1976	5.35	0.40	1999	1.72	3.19	2.00	2.20
1977	4.84	0.42	2000	1.61	2.84	2.22	1.67
			2001	1.10	2.30	1.64	1.65
			2002	1.06	2.23	1.84	1.41
			2003	0.90	2.64	2.07	1.93
			2004	0.81	2.20	1.65	1.52
			2005	0.58	2.19	1.48	1.34
			2006	0.62	2.38	1.03	1.46
			2007	0.60	2.92	0.98	1.53
			2008	0.81	3.23	1.56	1.65
			2009	1.42	3.23	2.89	2.05
			2010	1.22	3.54	2.22	2.25
			2011	1.47	3.30	2.79	2.62
			2012	1.24	2.92	1.62	2.17

*Note that the West Coast and South Coast boundaries for the ICSEAF data do not correspond exactly to the modern boundaries, but are closely related (see Figure 2.2 of Chapter 2).

Table 3.3a: The ***M. paradoxus*** survey abundance estimates in thousand tons are listed with their associated standard errors for the 0-500m depth range on the West Coast and South Coast (Fairweather 2012). Bold numbers indicate surveys for which the new gear was used on the *Africana*.

	West Coast				South Coast			
Year	Summer		Winter		Spring (Sep)		Autmn (Apr/May)	
1985	166.294	(35.299)	264.839	(52.949)	-	-	-	-
1986	196.111	(36.358)	172.477	(24.122)	13.758	(3.554)	-	-
1987	284.805	(53.101)	195.482	(44.415)	21.554	(4.605)	-	-
1988	158.758	(27.383)	233.041	(64.003)	-	-	30.316	(11.104)
1989	-	-	468.780	(124.830)	-	-	-	-
1990	282.174	(78.945)	226.862	(46.007)	-	-	-	-
1991	327.020	(82.180)	-	-	-	-	26.638	(10.460)
1992	226.687	(32.990)	-	-	-	-	24.304	(15.195)
1993	334.151	(50.234)	-	-	-	-	198.849	(98.452)
1994	330.270	(58.319)	-	-	-	-	111.469	(34.627)
1995	324.554	(80.357)	-	-	-	-	55.068	(22.380)
1996	430.908	(80.604)	-	-	-	-	85.546	(25.484)
1997	569.957	(108.200)	-	-	-	-	135.192	(51.031)
1998	-	-	-	-	-	-	-	-
1999	569.364	(114.536)	-	-	-	-	321.478	(113.557)
2000	-	-	-	-	-	-	-	-
2001	-	-	-	-	19.929	(9.956)	-	-
2002	267.487	(35.068)	-	-	-	-	-	-
2003	411.177	(69.431)	-	-	**88.442**	(36.051)	108.857	(37.528)
2004	**259.527**	(56.021)	-	-	**63.900**	(17.894)	**48.898**	(20.343)
2005	**286.416**	(39.849)	-	-	-	-	**26.605**	(7.952)
2006	315.310	(49.490)	-	-	72.415	(15.500)	34.799	(8.325)
2007	**397.049**	(71.564)	-	-	**52.287**	(19.231)	**129.646**	(60.661)
2008	**246.542**	(51.973)	-	-	**24.816**	(8.775)	**39.505**	(11.408)
2009	**330.235**	(28.526)	-	-	-	-	**102.834**	(28.670)
2010	589.533	(85.686)	-	-	-	-	169.560	(67.650)
2011	**347.082**	(92.540)	-	-	-	-	**24.105**	(7.089)
2012	**377.515**	(50.690)	-	-	-	-	-	-
2013	-	-	-	-	-	-	-	-

Table 3.3b: The ***M. capensis*** survey abundance estimates in thousand tons are listed with their associated standard errors for the 0-500m depth range on the West Coast and South Coast (Fairweather 2012). Bold numbers indicate surveys for which the new gear was used on the *Africana*.

	West Coast				South Coast			
Year	Summer		Winter		Spring (Sep)		Autmn (Apr/May)	
1985	125.028	(22.719)	181.487	(27.476)	-	-	-	-
1986	117.810	(23.636)	119.587	(18.489)	121.197	(16.625)	-	-
1987	75.693	(10.241)	87.391	(11.198)	159.088	(17.233)	-	-
1988	66.725	(10.765)	47.120	(9.568)	-	-	165.939	(21.871)
1989	-	-	323.833	(67.295)	-	-	-	-
1990	455.798	(135.237)	157.800	(23.561)	-	-	-	-
1991	77.357	(14.995)	-	-	-	-	274.298	(44.395)
1992	95.407	(11.744)	-	-	-	-	138.085	(15.357)
1993	92.598	(14.589)	-	-	-	-	158.340	(13.733)
1994	121.257	(35.951)	-	-	-	-	160.555	(23.701)
1995	199.142	(26.812)	-	-	-	-	236.025	(31.840)
1996	83.337	(9.285)	-	-	-	-	244.410	(25.107)
1997	257.293	(46.056)	-	-	-	-	183.087	(18.906)
1998	-	-	-	-	-	-	-	-
1999	196.992	(32.059)	-	-	-	-	191.203	(14.952)
2000	-	-	-	-	-	-	-	-
2001	-	-	-	-	133.793	(20.858)	-	-
2002	106.253	(15.813)	-	-	-	-	-	-
2003	75.960	(13.314)	-	-	**82.928**	(9.010)	128.450	(20.062)
2004	**205.939**	(33.216)	-	-	**106.119**	(15.596)	**99.902**	(12.027)
2005	**70.983**	(13.845)	-	-	-	-	**76.932**	(5.965)
2006	88.420	(22.851)	-	-	99.867	(9.803)	130.900	(14.816)
2007	**82.040**	(11.491)	-	-	**74.615**	(7.383)	**70.940**	(5.615)
2008	**50.877**	(5.355)	-	-	**94.232**	(11.456)	**108.195**	(9.978)
2009	**175.289**	(39.920)	-	-	-	-	**124.004**	(11.808)
2010	163.545	(34.444)	-	-	-	-	184.960	(37.720)
2011	**89.392**	(23.218)	-	-	-	-	**117.222**	(11.857)
2012	**92.588**	(11.926)	-	-	-	-	-	-
2013	-	-	-	-	-	-	-	-

Table 3.4a: The ***M. paradoxus*** survey proportions-at-length* for the **West Coast summer** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1985	0	0	0	0	0	0.01	0.02	0.03	0.04	0.11	0.22	0.16	0.11	0.08	0.06	0.04	0.03	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	0	0	0	0	0.01	0.02	0.03	0.04	0.05	0.11	0.17	0.16	0.1	0.1	0.08	0.06	0.03	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1987	0	0	0	0	0	0.01	0.04	0.05	0.09	0.19	0.21	0.15	0.08	0.05	0.04	0.03	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1988	0	0	0	0.01	0.02	0.05	0.11	0.12	0.13	0.16	0.11	0.11	0.07	0.03	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1990	0	0	0	0	0.02	0.03	0.03	0.09	0.15	0.17	0.1	0.08	0.1	0.09	0.06	0.03	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991	0	0	0	0	0.01	0.02	0.04	0.1	0.2	0.16	0.12	0.08	0.09	0.07	0.04	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992	0	0	0	0	0.01	0.03	0.08	0.14	0.1	0.1	0.13	0.13	0.09	0.06	0.04	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0	0.01	0.01	0.02	0.05	0.07	0.09	0.18	0.18	0.1	0.08	0.05	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	0	0	0	0	0.01	0.02	0.04	0.07	0.1	0.14	0.13	0.09	0.09	0.08	0.06	0.05	0.03	0.02	0.01	0.01	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1995	0	0	0	0	0.02	0.09	0.23	0.2	0.17	0.1	0.05	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996	0	0	0.01	0.06	0.1	0.15	0.22	0.16	0.1	0.06	0.03	0.03	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1997	0	0	0	0	0.02	0.1	0.12	0.17	0.21	0.12	0.11	0.08	0.04	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1999	0	0	0	0.01	0.07	0.1	0.13	0.16	0.16	0.09	0.09	0.07	0.05	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2002	0	0	0	0	0.01	0.04	0.09	0.09	0.1	0.13	0.14	0.12	0.08	0.05	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0	0	0.01	0.03	0.06	0.09	0.11	0.11	0.09	0.12	0.14	0.1	0.06	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2004	0	0	0.02	0.04	0.06	0.07	0.05	0.06	0.1	0.12	0.11	0.09	0.07	0.05	0.04	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2005	0	0	0.01	0.02	0.05	0.11	0.22	0.17	0.09	0.07	0.09	0.06	0.03	0.02	0.02	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2006	0	0	0.01	0.02	0.04	0.07	0.08	0.11	0.14	0.13	0.12	0.1	0.09	0.04	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2007	0	0	0.02	0.04	0.04	0.05	0.1	0.1	0.12	0.1	0.08	0.08	0.06	0.05	0.03	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2008	0	0	0.02	0.02	0.04	0.07	0.08	0.07	0.09	0.14	0.09	0.05	0.06	0.06	0.04	0.04	0.04	0.03	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	0	0	0.01	0.02	0.04	0.12	0.2	0.14	0.09	0.08	0.07	0.05	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	0	0	0.01	0.01	0.03	0.08	0.15	0.1	0.09	0.1	0.09	0.09	0.08	0.05	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	0	0	0.01	0.03	0.05	0.07	0.07	0.17	0.21	0.11	0.04	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2012	0	0	0	0.01	0.02	0.06	0.14	0.16	0.09	0.08	0.11	0.08	0.07	0.06	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4b: The ***M. capensis*** survey proportions-at-length for the **West Coast summer** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1985	0	0	0	0.01	0.02	0.02	0.05	0.03	0.02	0.13	0.33	0.22	0.08	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	0	0	0	0.01	0.01	0.01	0.01	0.02	0.05	0.12	0.14	0.14	0.15	0.12	0.09	0.05	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1987	0	0	0	0.01	0.02	0.01	0	0.01	0.04	0.04	0.05	0.06	0.12	0.15	0.11	0.07	0.04	0.03	0.04	0.05	0.05	0.04	0.03	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1988	0	0	0.01	0.07	0.36	0.19	0.04	0.03	0.03	0.02	0.02	0.02	0.03	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1990	0	0	0	0	0	0.01	0.01	0.12	0.3	0.3	0.16	0.05	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991	0	0	0	0.01	0.05	0.04	0.04	0.04	0.04	0.09	0.21	0.18	0.12	0.06	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992	0	0	0	0.02	0.08	0.1	0.08	0.06	0.05	0.04	0.04	0.05	0.08	0.09	0.07	0.04	0.03	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0.02	0.06	0.05	0.02	0.01	0.01	0.01	0.01	0.03	0.07	0.1	0.1	0.1	0.09	0.06	0.03	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	0	0	0.02	0.14	0.02	0.02	0.02	0.03	0.02	0.03	0.05	0.06	0.07	0.08	0.06	0.04	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1995	0	0	0	0	0.01	0.01	0.03	0.1	0.22	0.23	0.14	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.01	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996	0	0	0	0.05	0.15	0.17	0.08	0.07	0.09	0.03	0.02	0.05	0.06	0.04	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1997	0	0	0.01	0.03	0.01	0.01	0.01	0.03	0.05	0.1	0.22	0.23	0.14	0.07	0.03	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1999	0	0.05	0.49	0.25	0.08	0.06	0.02	0.01	0	0	0	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2002	0	0	0	0.02	0.05	0.1	0.09	0.2	0.23	0.09	0.05	0.04	0.02	0.01	0.01	0.01	0.01	0	0	0.01	0.01	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0.01	0.04	0.13	0.13	0.09	0.07	0.06	0.07	0.09	0.07	0.05	0.03	0.02	0.01	0.01	0.01	0	0	0	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2004	0	0	0.01	0.01	0.01	0.04	0.1	0.14	0.28	0.23	0.1	0.04	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2005	0	0.03	0.16	0.32	0.19	0.02	0.01	0.01	0.01	0.02	0.06	0.08	0.04	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2006	0	0.01	0.08	0.07	0.05	0.05	0.1	0.16	0.11	0.06	0.05	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2007	0	0	0.01	0.01	0.02	0.01	0.02	0.04	0.05	0.13	0.23	0.19	0.12	0.08	0.04	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2008	0	0.01	0.06	0.05	0.06	0.06	0.08	0.1	0.04	0.02	0.02	0.03	0.03	0.04	0.03	0.02	0.02	0.02	0.03	0.05	0.06	0.06	0.05	0.03	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	0	0	0.04	0.04	0.03	0.02	0.02	0.02	0.09	0.27	0.3	0.12	0.03	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	0	0	0.01	0.02	0.03	0.05	0.1	0.38	0.22	0.05	0.03	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	0	0.01	0.05	0.22	0.2	0.07	0.01	0	0.01	0.02	0.05	0.06	0.05	0.05	0.03	0.02	0.01	0.01	0	0	0	0.01	0.01	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2012	0	0	0.01	0.02	0.02	0.04	0.11	0.22	0.17	0.12	0.12	0.06	0.02	0.01	0.01	0.01	0	0	0	0	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

*The generally lower numbers of large *M. paradoxus* fish caught in the surveys is most likely as a result of a higher natural and fishing mortality experienced by this species.

Table 3.4c: The ***M. paradoxus*** survey proportions-at-length for the **West Coast winter** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1985	0	0	0	0	0	0.01	0.01	0.03	0.06	0.07	0.1	0.1	0.16	0.16	0.12	0.06	0.04	0.02	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	0	0	0	0	0.01	0.03	0.08	0.14	0.1	0.11	0.11	0.09	0.09	0.09	0.05	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1987	0	0	0	0.01	0.02	0.04	0.08	0.1	0.09	0.08	0.11	0.12	0.14	0.09	0.04	0.03	0.01	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1988	0	0	0.01	0.01	0.01	0.03	0.08	0.1	0.07	0.08	0.11	0.12	0.12	0.08	0.03	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1989	0	0	0	0	0.03	0.08	0.06	0.05	0.05	0.06	0.12	0.13	0.13	0.1	0.06	0.04	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1990	0	0	0	0	0.02	0.09	0.13	0.1	0.1	0.11	0.09	0.09	0.07	0.04	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4d: The ***M. capensis*** survey proportions-at-length for the **West Coast winter** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1985	0	0	0	0	0	0	0.03	0.19	0.29	0.18	0.08	0.04	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	0	0	0	0	0	0	0	0.03	0.11	0.15	0.09	0.06	0.06	0.07	0.08	0.08	0.08	0.06	0.04	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1987	0	0	0	0	0	0.01	0.04	0.14	0.23	0.09	0.04	0.05	0.04	0.03	0.03	0.03	0.04	0.04	0.04	0.03	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1988	0	0	0	0.01	0.02	0.01	0.01	0.06	0.17	0.23	0.18	0.08	0.04	0.02	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1989	0	0	0	0	0.06	0.16	0.14	0.3	0.21	0.06	0.03	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1990	0	0	0	0	0.01	0.03	0.07	0.1	0.09	0.1	0.2	0.12	0.05	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4e: The ***M. paradoxus*** survey proportions-at-length for the **South Coast spring** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1986	0	0	0	0	0	0.01	0.01	0.01	0.01	0.03	0.04	0.04	0.08	0.14	0.18	0.13	0.11	0.08	0.04	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1987	0	0	0	0	0	0	0	0	0	0	0.01	0.1	0.24	0.24	0.13	0.05	0.04	0.02	0.03	0.02	0.03	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2001	0	0	0	0	0	0	0	0	0	0.01	0.07	0.21	0.22	0.21	0.14	0.06	0.03	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0	0.02	0.02	0	0	0	0	0	0.02	0.11	0.21	0.25	0.17	0.08	0.03	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2004	0	0	0	0	0.01	0.01	0	0	0	0.01	0.01	0.07	0.18	0.2	0.13	0.08	0.04	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2006	0	0	0	0	0	0	0	0	0	0	0.01	0.08	0.19	0.23	0.19	0.1	0.05	0.03	0.02	0.01	0.01	0.01	0	0.01	0	0.01	0.01	0	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2007	0	0	0	0	0	0	0	0	0.01	0.02	0.01	0.03	0.14	0.25	0.21	0.13	0.07	0.04	0.03	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2008	0	0	0	0	0	0	0	0	0.01	0.01	0.01	0.05	0.16	0.23	0.17	0.12	0.08	0.05	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4f: The ***M. capensis*** survey proportions-at-length for the **South Coast spring** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1986	0	0	0	0.01	0.04	0.07	0.05	0.02	0.01	0.01	0.02	0.03	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1987	0	0	0	0.02	0.05	0.04	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.04	0.04	0.04	0.05	0.06	0.06	0.05	0.04	0.04	0.04	0.04	0.04	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2001	0	0	0.01	0.04	0.07	0.04	0.02	0.02	0.02	0.01	0.01	0.01	0.02	0.03	0.03	0.04	0.05	0.07	0.08	0.08	0.07	0.06	0.04	0.04	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0.02	0.04	0.04	0.04	0.04	0.02	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.04	0.04	0.04	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2004	0	0.02	0.05	0.07	0.05	0.02	0.01	0.01	0.01	0.01	0.03	0.04	0.05	0.06	0.05	0.04	0.03	0.03	0.04	0.05	0.05	0.05	0.04	0.04	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2006	0	0	0.02	0.03	0.04	0.03	0.01	0.01	0.03	0.04	0.05	0.05	0.04	0.05	0.06	0.07	0.07	0.07	0.06	0.05	0.04	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2007	0	0	0.01	0.03	0.06	0.05	0.03	0.01	0.01	0.02	0.03	0.06	0.09	0.09	0.07	0.05	0.05	0.05	0.04	0.04	0.04	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2008	0	0.01	0.03	0.07	0.1	0.08	0.04	0.02	0.02	0.02	0.02	0.03	0.04	0.04	0.05	0.06	0.05	0.04	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4g: The ***M. paradoxus*** survey proportions-at-length for the **South Coast autumn** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1988	0	0	0	0	0	0	0	0	0.01	0.02	0.01	0.01	0.03	0.09	0.12	0.13	0.15	0.13	0.08	0.06	0.05	0.03	0.03	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992	0	0	0	0	0	0	0	0	0	0	0	0.04	0.12	0.22	0.25	0.16	0.08	0.03	0.03	0.02	0.01	0.01	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0	0	0	0.01	0	0	0	0	0.02	0.07	0.16	0.2	0.17	0.11	0.07	0.04	0.02	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	0	0	0	0.01	0.01	0.01	0	0.01	0.03	0.04	0.07	0.11	0.14	0.13	0.1	0.07	0.03	0.02	0.01	0	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0
1995	0	0	0	0	0	0	0	0	0	0	0.02	0.04	0.08	0.15	0.22	0.16	0.1	0.06	0.04	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996	0	0	0	0	0	0	0	0	0	0	0	0.02	0.1	0.23	0.24	0.16	0.08	0.04	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1997	0	0	0	0	0	0	0	0	0	0.01	0.01	0.06	0.09	0.12	0.13	0.13	0.12	0.07	0.03	0.02	0.01	0.01	0.01	0.02	0.02	0.03	0.03	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1999	0	0	0	0	0	0	0	0	0	0	0.02	0.06	0.1	0.17	0.16	0.12	0.09	0.07	0.06	0.04	0.03	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0	0	0	0	0	0	0	0	0.02	0.07	0.17	0.2	0.12	0.09	0.05	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2004	0	0	0	0.01	0.03	0.05	0.03	0.01	0	0.01	0.02	0.05	0.09	0.12	0.12	0.13	0.12	0.08	0.06	0.04	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2005	0	0	0	0	0.01	0.01	0.02	0.01	0	0.01	0.02	0.07	0.07	0.08	0.09	0.11	0.11	0.09	0.05	0.03	0.03	0.03	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2006	0	0	0	0	0	0	0	0	0	0	0.01	0.07	0.18	0.23	0.18	0.09	0.06	0.04	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2007	0	0	0	0	0.03	0.03	0.01	0	0.01	0.01	0.01	0.05	0.12	0.14	0.11	0.09	0.09	0.08	0.06	0.04	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2008	0	0	0	0.01	0.03	0.02	0.01	0	0	0	0.03	0.09	0.09	0.09	0.12	0.13	0.11	0.08	0.06	0.04	0.03	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	0	0	0	0	0	0	0	0	0	0	0.01	0.03	0.04	0.05	0.08	0.12	0.18	0.16	0.12	0.07	0.06	0.03	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	0	0	0	0	0	0	0	0	0	0	0.01	0.04	0.1	0.13	0.13	0.14	0.12	0.09	0.07	0.05	0.04	0.03	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	0	0	0	0	0	0	0	0	0	0	0	0.02	0.08	0.13	0.13	0.11	0.1	0.08	0.05	0.03	0.03	0.02	0.02	0.02	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0	0.01	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4h: The ***M. capensis*** survey proportions-at-length for the **South Coast autumn** surveys are listed by 2cm length classes.

Year	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1988	0	0	0	0.01	0.03	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.05	0.06	0.06	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.03	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992	0	0	0	0	0.01	0.03	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.04	0.04	0.04	0.03	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0	0	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.04	0.06	0.07	0.09	0.09	0.08	0.06	0.05	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	0	0	0.01	0.01	0.02	0.02	0.04	0.03	0.02	0.02	0.02	0.02	0.03	0.05	0.05	0.05	0.05	0.04	0.03	0.02	0.03	0.04	0.04	0.04	0.04	0.04	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1995	0	0	0	0.01	0.02	0.03	0.04	0.05	0.05	0.05	0.04	0.04	0.03	0.04	0.04	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996	0	0	0	0.01	0.01	0.03	0.05	0.04	0.03	0.02	0.02	0.02	0.02	0.03	0.04	0.04	0.04	0.06	0.07	0.07	0.06	0.06	0.05	0.05	0.04	0.03	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1997	0	0	0	0.02	0.03	0.04	0.04	0.03	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.05	0.05	0.05	0.05	0.05	0.04	0.04	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1999	0	0	0	0.01	0.03	0.03	0.04	0.03	0.02	0.03	0.05	0.06	0.05	0.03	0.03	0.04	0.06	0.06	0.06	0.05	0.04	0.04	0.03	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0	0.01	0.02	0.02	0.04	0.04	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.05	0.06	0.06	0.05	0.05	0.06	0.06	0.06	0.05	0.04	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2004	0	0	0	0.02	0.04	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.05	0.05	0.05	0.06	0.06	0.07	0.06	0.06	0.05	0.04	0.04	0.03	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2005	0	0	0.01	0.01	0.02	0.03	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.05	0.06	0.06	0.07	0.07	0.06	0.05	0.05	0.04	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2006	0	0	0	0	0.01	0.02	0.02	0.02	0.02	0.03	0.04	0.05	0.05	0.06	0.07	0.08	0.07	0.06	0.05	0.04	0.04	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2007	0	0	0.01	0.03	0.06	0.06	0.04	0.03	0.03	0.03	0.03	0.04	0.06	0.07	0.07	0.06	0.05	0.06	0.05	0.04	0.04	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2008	0	0	0	0.01	0.01	0.03	0.02	0.02	0.02	0.03	0.04	0.05	0.05	0.04	0.04	0.05	0.06	0.07	0.08	0.07	0.05	0.05	0.04	0.04	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	0	0	0.01	0.03	0.03	0.02	0.01	0.01	0.02	0.02	0.02	0.03	0.04	0.06	0.09	0.11	0.08	0.06	0.05	0.05	0.05	0.04	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	0	0	0.01	0.05	0.05	0.06	0.03	0.02	0.02	0.02	0.03	0.03	0.04	0.05	0.06	0.05	0.05	0.05	0.04	0.05	0.05	0.05	0.04	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	0	0.01	0.03	0.02	0.03	0.05	0.03	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.05	0.06	0.07	0.07	0.06	0.05	0.04	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.5a: Species-combined **West Coast offshore** catches-at-length (as percentage frequencies) are listed by 2cm length classes.

Year	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1981	0.6	2.6	5.9	11.9	16.8	15.9	12.0	8.6	6.5	4.7	3.1	2.3	1.9	1.3	1.1	0.9	0.7	0.6	0.5	0.4	0.3	0.3	0.2	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1982	0.3	2.5	7.6	12.0	15.3	16.6	13.0	9.3	5.9	4.6	2.8	1.8	1.5	1.2	1.2	1.0	0.8	0.6	0.4	0.3	0.3	0.2	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1983	<0.1	0.5	1.8	5.4	8.8	10.4	12.6	12.7	11.0	8.7	6.5	4.4	3.4	2.8	2.4	2.0	1.5	1.2	0.9	0.7	0.5	0.4	0.3	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-
1984	-	0.3	0.9	5.7	11.3	12.7	13.9	11.1	9.2	8.2	6.2	3.6	2.9	2.5	2.3	1.9	1.4	1.0	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-
1985	-	<0.1	0.1	0.4	1.5	4.3	11.5	14.6	13.2	11.9	9.6	7.1	5.2	3.6	2.9	2.5	1.8	1.7	1.4	1.3	1.1	0.9	0.7	0.6	0.5	0.5	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-
1986	-	-	0.2	0.8	2.9	5.0	9.4	13.6	14.7	13.4	11.1	7.5	5.0	3.3	2.6	1.9	1.5	1.1	0.9	0.8	0.6	0.6	0.6	0.5	0.5	0.4	0.4	0.3	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1
1987	-	<0.1	0.4	2.7	7.1	11.9	14.0	13.7	10.7	7.2	5.8	4.6	3.9	3.6	2.9	2.6	1.9	1.6	1.2	1.0	0.8	0.6	0.4	0.3	0.3	0.2	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	<0.1
1988	-	<0.1	0.9	3.6	10.7	14.1	15.7	12.9	10.2	7.4	5.0	3.8	2.8	2.0	1.7	1.5	1.2	1.1	0.9	0.9	0.7	0.7	0.6	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-
1989	<0.1	0.3	1.8	5.5	11.5	15.8	16.1	12.2	8.8	6.5	4.5	3.3	2.6	2.0	1.7	1.3	1.0	0.8	0.7	0.7	0.6	0.6	0.5	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-
1990	-	<0.1	0.5	1.3	5.8	10.6	13.1	14.1	12.7	11.5	8.1	5.5	4.2	3.0	2.3	1.6	1.1	1.0	0.7	0.6	0.4	0.4	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-
1991	-	0.1	0.6	2.2	4.9	7.7	9.2	9.9	8.8	8.8	7.5	6.6	6.3	5.2	4.1	3.2	2.4	1.9	1.4	1.4	1.1	1.2	1.1	1.0	0.8	0.7	0.5	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-
1992	<0.1	0.2	1.0	4.1	9.2	12.2	12.4	10.7	8.2	6.8	5.3	4.5	3.6	3.1	3.2	2.6	2.3	2.3	1.7	1.5	1.1	0.9	0.7	0.6	0.5	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-
1993	-	0.1	0.3	1.5	4.1	7.5	9.5	8.5	7.1	6.9	7.3	6.4	6.5	6.3	6.6	5.1	3.8	3.4	2.3	1.9	1.2	0.9	0.6	0.5	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-
1994	-	<0.1	0.1	0.5	2.7	7.7	11.8	13.1	8.0	8.0	6.9	5.3	4.2	4.2	4.4	4.6	4.6	4.1	2.9	2.1	1.2	1.1	0.6	0.5	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1995	-	0.3	1.9	3.5	5.4	7.1	12.2	11.8	11.9	10.9	8.5	4.8	3.2	3.6	2.3	1.3	1.6	1.5	1.4	1.5	1.4	1.0	0.9	0.6	0.4	0.3	0.3	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-
1996	<0.1	0.4	1.7	4.3	5.7	9.6	11.6	12.1	11.0	9.7	8.2	6.2	4.2	3.1	2.1	1.9	1.1	1.2	0.9	0.9	0.8	0.7	0.5	0.5	0.3	0.3	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-
1997	<0.1	0.3	1.8	4.0	6.0	9.6	13.0	11.8	11.1	9.7	8.0	5.2	3.6	3.3	2.1	1.4	1.2	1.3	1.1	1.2	1.0	0.8	0.7	0.5	0.3	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1998	<0.1	0.2	1.2	2.8	4.5	7.3	11.2	11.9	12.0	10.9	8.8	6.0	4.3	3.9	2.5	1.7	1.5	1.6	1.4	1.5	1.2	1.0	0.8	0.5	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1999	<0.1	0.2	1.1	2.6	4.4	7.6	11.6	11.7	11.5	10.3	8.4	5.6	4.0	3.7	2.5	1.8	1.7	1.8	1.6	1.7	1.5	1.2	1.0	0.7	0.5	0.4	0.4	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
2005	<0.1	<0.1	0.8	6.8	17.2	17.0	15.0	11.6	6.4	4.2	2.6	2.0	2.4	2.1	2.2	1.6	1.2	1.2	1.1	1.0	0.8	0.7	0.5	0.5	0.3	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-
2006	-	<0.1	0.8	3.8	7.5	11.5	14.5	14.4	13.7	9.4	4.2	3.2	2.4	2.2	2.0	1.7	1.6	1.4	1.2	1.0	0.6	0.6	0.5	0.5	0.3	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	<0.1
2007	-	-	0.2	1.5	6.2	11.5	15.6	16.7	14.1	9.9	4.8	2.8	2.2	2.2	2.0	1.9	1.5	1.4	1.3	1.0	0.7	0.6	0.5	0.5	0.3	0.2	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-
2008	-	-	<0.1	0.4	2.2	6.1	11.3	15.7	12.5	10.8	8.5	4.4	5.0	4.3	3.0	2.5	2.8	2.3	2.0	1.6	1.2	0.9	0.8	0.7	0.3	0.3	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	<0.1
2009	-	<0.1	0.7	2.3	4.9	9.5	10.5	12.3	10.4	7.3	4.8	4.3	4.8	3.7	3.7	3.9	3.7	3.2	2.5	1.9	1.5	1.1	1.0	0.8	0.4	0.2	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	<0.1	-	-	-
2010	-	0.2	0.2	0.5	1.7	6.6	13.0	13.7	11.3	9.0	6.3	4.5	4.3	4.6	4.7	4.5	3.2	3.1	1.9	1.6	1.2	1.0	0.8	0.7	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-
2011	-	0.5	0.2	0.2	1.4	5.5	10.1	12.6	11.8	11.2	8.6	6.0	5.2	4.4	4.1	3.6	2.4	2.4	1.9	1.7	1.3	1.2	0.9	0.8	0.5	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-
2012	-	0.4	0.9	1.9	3.4	8.6	12.3	9.4	8.7	7.8	5.8	5.9	6.4	5.0	5.0	4.3	3.3	2.7	1.9	1.5	1.1	1.0	0.7	0.5	0.4	0.3	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-

Table 3.5b: Species-combined **South Coast offshore** catches-at-length (as percentage frequencies) are listed by 2cm length classes.

Year	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1975	-	-	-	0.2	0.9	2.1	4.6	5.5	4.7	5.6	4.5	6.6	6.8	6.8	7.5	6.7	6.8	5.5	5.5	4.4	3.1	2.4	1.6	1.3	1.3	1.1	0.6	0.6	0.5	0.5	0.5	0.5	0.3	0.3	0.2	0.2	0.1	-	-	-	-	-	-	-
1976	-	0.5	0.7	1.7	3.6	11.3	20.8	16.6	11.3	6.6	3.3	5.0	3.7	3.3	4.0	3.2	1.8	0.8	0.5	0.3	0.2	0.2	0.1	<0.1	0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1977	-	<0.1	<0.1	0.2	0.3	1.5	4.5	5.0	5.8	7.2	7.3	7.8	6.8	6.1	4.2	3.6	3.0	2.6	2.6	2.2	2.2	2.4	1.8	1.1	0.9	6.1	4.4	3.5	4.5	2.1	<0.1	<0.1	-	<0.1	-	<0.1	<0.1	-	-	-	-	-	-	-	-
1978	-	0.3	0.7	2.7	6.3	13.8	15.7	13.8	10.4	7.7	5.2	4.0	3.2	2.6	2.7	2.0	1.6	1.4	1.0	0.7	0.7	0.7	0.4	0.5	0.3	0.2	0.3	0.2	0.2	0.1	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-
1979	-	-	-	-	-	<0.1	0.4	1.3	3.6	5.3	5.6	4.8	5.0	4.9	6.3	7.9	8.1	6.3	6.9	5.8	5.0	4.0	3.4	2.7	2.9	2.0	1.9	1.4	1.0	0.8	0.7	0.7	0.3	0.3	<0.1	<0.1	0.2	<0.1	-	-	-	-	-	-	-
1980	-	-	0.4	1.7	5.2	8.4	11.3	11.1	10.1	7.7	7.0	6.0	5.3	4.5	3.7	3.0	2.7	1.9	1.5	1.4	1.4	1.0	0.9	0.8	0.7	0.5	0.5	0.4	0.3	0.2	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-	-
1981	-	<0.1	0.6	2.1	4.1	9.8	11.9	10.7	10.7	7.1	7.8	6.5	5.5	4.1	3.9	3.0	2.5	2.0	1.6	1.2	1.2	0.9	0.6	0.5	0.3	0.3	0.3	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-
1982	<0.1	0.4	1.2	2.5	5.4	9.7	10.8	9.2	7.8	5.8	5.5	5.5	4.5	3.7	3.6	3.6	3.0	2.7	2.4	2.2	2.1	1.9	1.5	1.2	0.9	0.7	0.6	0.5	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1
1983	-	0.1	0.3	1.9	4.6	7.6	8.1	9.0	10.8	9.4	8.0	5.3	4.5	3.9	4.2	3.7	3.6	3.1	2.3	1.9	1.7	1.5	1.2	1.0	0.7	0.5	0.3	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
1984	<0.1	0.2	1.3	3.1	9.6	12.6	14.2	10.6	7.5	5.5	5.6	4.3	4.2	3.4	2.6	2.1	1.8	1.9	1.7	1.4	1.1	1.0	0.8	0.7	0.7	0.6	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1985	-	-	<0.1	0.4	2.5	6.3	11.2	11.7	10.4	10.1	8.6	6.0	4.7	3.4	2.9	2.8	2.5	2.6	2.3	2.0	1.7	1.3	1.3	1.3	0.9	0.7	0.7	0.6	0.4	0.3	0.1	0.2	0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-
1986	-	-	-	0.2	1.1	4.4	10.2	10.0	10.5	6.9	8.3	6.4	6.2	5.0	4.2	3.7	2.9	2.8	2.6	2.4	2.5	2.1	1.6	1.6	1.0	0.7	0.8	0.7	0.4	0.4	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1987	-	-	<0.1	0.4	3.3	8.4	11.8	12.5	9.0	7.4	5.4	3.7	3.7	3.8	3.8	3.6	3.2	2.9	3.0	2.5	2.3	2.1	1.7	1.2	0.9	0.8	0.7	0.6	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-
1988	-	<0.1	0.5	2.6	4.5	8.1	10.2	11.3	11.0	7.0	4.9	4.1	4.3	4.0	3.8	3.6	2.7	2.6	2.6	2.0	2.2	1.9	1.4	1.4	0.9	0.7	0.5	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1989	-	0.2	0.3	2.0	8.4	13.2	17.1	13.0	7.1	6.3	4.7	3.7	3.3	2.3	2.1	1.6	2.0	2.3	1.6	1.7	1.5	1.6	1.2	1.0	0.7	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-
1990	<0.1	<0.1	0.4	1.0	4.0	7.3	8.7	10.0	9.2	10.4	9.5	7.6	6.1	5.1	4.0	2.9	2.3	2.2	1.6	1.5	1.1	1.1	0.9	0.8	0.7	0.5	0.4	0.2	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-
1991	-	<0.1	0.5	2.0	4.7	8.1	10.8	12.1	10.8	10.0	7.7	6.1	5.1	4.2	3.1	2.3	1.8	1.7	1.4	1.3	1.0	1.0	0.9	0.7	0.6	0.5	0.3	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-
1992	<0.1	<0.1	0.5	2.1	4.8	7.0	8.6	10.6	10.7	10.5	8.9	7.8	5.5	4.3	3.5	2.5	1.9	1.8	1.4	1.4	1.0	1.0	0.8	0.7	0.7	0.5	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-
1993	-	0.1	0.4	2.2	5.4	8.8	10.5	10.4	9.8	9.4	9.4	6.8	5.3	3.8	3.3	2.4	1.8	1.7	1.3	1.3	1.0	0.9	0.8	0.6	0.6	0.5	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-
1994	-	<0.1	0.2	1.3	3.8	8.2	11.6	13.9	10.4	9.8	7.7	5.5	3.8	3.3	3.1	2.7	2.6	2.3	1.8	1.5	1.0	1.1	0.8	0.7	0.7	0.6	0.6	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	<0.1	-
1995	-	0.1	1.1	2.1	4.4	6.1	11.1	13.3	12.9	10.8	7.3	4.2	3.6	4.0	2.2	1.2	1.2	1.4	1.2	1.9	1.6	1.5	1.5	1.3	1.1	0.9	0.9	0.5	0.4	0.2	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-
1996	-	<0.1	0.2	0.4	2.2	5.0	10.1	12.2	14.2	14.1	10.8	8.0	4.7	3.2	2.3	1.8	1.3	1.5	1.4	1.3	1.0	0.9	0.7	0.6	0.5	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-

Table 3.5c: South Coast inshore catches-at-length (as percentage frequencies), assumed to be *M. capensis* only, are listed by 2cm length classes.

Year	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1981	-	-	-	<0.1	0.3	1.4	3.7	7.0	10.1	11.7	11.9	10.3	9.4	7.5	6.0	4.9	3.6	3.1	2.1	1.7	1.5	1.1	0.8	0.6	0.4	0.3	0.2	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-
1982	-	-	-	0.1	0.6	3.1	8.5	13.3	14.4	12.5	11.2	8.8	6.7	5.2	3.8	2.9	2.3	1.6	1.2	1.0	0.7	0.6	0.4	0.3	0.2	0.2	0.1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1983	-	-	-	<0.1	<0.1	0.4	1.8	4.0	6.6	8.4	9.2	9.7	10.2	10.5	9.6	8.0	6.1	4.6	3.2	2.2	1.5	1.1	0.8	0.6	0.4	0.3	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1984	-	-	-	-	<0.1	0.3	1.7	5.0	8.6	11.4	13.2	13.9	12.1	8.3	5.8	4.3	3.5	2.8	2.2	1.8	1.6	1.2	0.9	0.6	0.4	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-
1985	-	-	-	<0.1	<0.1	0.2	0.6	1.6	3.6	5.5	6.8	8.3	10.0	11.6	10.6	9.7	8.7	6.3	4.5	3.2	2.5	2.0	1.4	1.0	0.6	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-
1986	-	-	<0.1	<0.1	<0.1	0.5	1.9	4.8	8.1	10.2	9.6	9.0	7.2	6.7	5.9	5.4	5.5	5.2	4.7	4.2	3.6	2.5	1.7	1.1	0.7	0.4	0.3	0.2	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-
1987	-	-	-	-	<0.1	0.3	1.0	2.9	6.1	9.9	11.0	13.6	11.3	8.6	6.5	5.5	4.6	4.0	3.1	2.6	2.5	2.3	1.4	1.0	0.6	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-
1988	-	-	<0.1	<0.1	0.6	2.1	5.1	9.3	9.7	9.3	8.5	8.2	8.1	6.9	6.2	5.2	4.7	3.6	3.1	2.4	2.1	1.9	1.0	0.7	0.5	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-	-	-
1989	-	<0.1	<0.1	0.2	0.8	2.4	5.1	8.2	9.7	10.2	10.2	9.9	8.0	6.5	5.5	5.2	4.0	3.2	2.4	2.3	1.8	1.6	0.9	0.6	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-
1990	-	-	-	<0.1	0.3	1.0	2.4	4.8	6.4	7.5	9.5	10.6	11.1	8.9	7.8	6.8	5.3	4.0	3.2	2.9	2.2	1.6	1.2	0.8	0.5	0.4	0.2	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	<0.1	-	-	-	-
1991	-	-	<0.1	<0.1	0.3	1.0	2.3	4.3	6.5	7.5	7.5	7.7	8.0	8.5	8.3	7.7	6.7	5.9	4.4	3.9	2.8	2.1	1.5	1.1	0.7	0.5	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-
1992	-	<0.1	0.2	0.6	1.5	3.5	5.8	7.7	8.2	8.3	8.2	7.4	7.3	6.6	6.3	5.5	5.1	4.3	3.3	3.0	2.3	1.7	1.1	0.7	0.5	0.3	0.2	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-
1993	-	-	<0.1	0.2	0.5	1.4	3.1	6.6	7.0	7.9	9.2	11.1	12.2	9.4	7.0	6.0	4.9	3.4	2.3	2.2	1.9	1.3	0.8	0.5	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-	-	-	-
1994	-	<0.1	<0.1	0.3	1.0	3.2	4.6	7.3	8.4	8.4	7.7	7.3	6.9	6.1	5.8	6.6	5.2	3.9	3.6	3.5	3.1	2.5	1.7	1.0	0.6	0.4	0.2	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-	-	-	-
1995	-	-	<0.1	<0.1	0.5	1.5	3.6	4.8	7.9	9.1	9.1	9.3	9.0	8.4	7.2	6.5	5.3	4.0	2.8	2.4	2.0	1.8	1.4	1.1	0.9	0.6	0.4	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-
1996	-	<0.1	<0.1	0.2	0.8	2.1	6.2	7.8	9.5	13.0	11.7	8.9	9.2	6.5	5.1	4.8	3.5	2.4	1.9	1.6	1.3	1.2	0.9	0.6	0.4	0.3	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-
1998	-	-	-	<0.1	0.4	2.2	5.6	8.2	14.6	13.2	10.5	7.6	6.4	6.3	4.9	4.5	3.7	2.7	2.2	1.5	1.2	1.1	0.7	0.8	0.6	0.4	0.3	0.2	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1999	-	-	<0.1	<0.1	0.5	1.4	3.7	6.6	7.8	11.8	12.4	9.8	9.2	8.0	6.6	5.2	3.5	3.4	2.0	2.1	1.2	1.1	0.8	0.8	0.7	0.6	0.5	0.3	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	<0.1	-	-	-	-	-	-	-	-
2000	-	<0.1	<0.1	<0.1	0.4	0.9	2.9	6.4	8.5	10.8	11.7	10.6	9.6	7.9	7.5	5.9	4.6	3.4	2.2	1.8	1.0	1.0	0.8	0.6	0.5	0.4	0.4	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-	-	-	-	-	-	-
2001	-	-	<0.1	<0.1	0.4	1.5	4.9	9.5	13.7	13.1	10.9	8.0	6.4	4.6	3.2	2.8	2.8	2.4	2.5	2.8	2.5	2.1	1.9	1.1	0.9	0.7	0.5	0.5	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-
2007	-	<0.1	0.3	1.0	2.6	6.3	9.1	11.8	11.4	10.3	9.1	7.0	4.9	3.7	3.4	3.0	3.1	2.4	2.1	1.9	1.8	1.4	1.1	0.5	0.4	0.3	0.5	0.3	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-
2008	-	0.2	0.2	0.7	2.5	6.7	9.3	9.1	10.0	9.0	8.4	7.0	5.8	4.6	4.2	3.9	3.4	3.2	2.5	2.6	2.0	1.6	1.3	0.6	0.4	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	<0.1	-	-	-	-
2009	-	<0.1	0.2	1.2	3.3	7.1	9.3	8.6	8.3	9.8	8.6	7.2	5.3	5.0	4.5	3.8	3.5	3.1	2.5	2.6	2.0	1.6	1.1	0.6	0.3	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-
2010	<0.1	<0.1	0.4	1.4	3.7	7.0	9.9	10.7	8.1	8.6	7.9	6.3	5.2	4.4	3.9	3.5	3.3	3.6	2.6	2.8	2.0	1.5	1.2	0.7	0.4	0.3	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	-	-	-	-
2011	-	<0.1	0.4	1.3	3.1	7.3	9.3	9.9	8.9	9.5	9.8	7.7	5.6	4.5	3.8	3.3	3.2	2.7	2.2	2.2	1.6	1.3	0.8	0.5	0.3	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-	-
2012	<0.1	0.2	0.5	1.7	3.8	7.0	9.7	10.8	9.5	8.3	8.1	6.9	5.5	4.8	4.4	3.5	2.7	2.7	2.1	2.1	1.6	1.3	1.0	0.5	0.4	0.3	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	-	<0.1	-	-	-	-	-

Table 3.5d: Species-combined **West Coast longline** catches-at-length (as percentage frequencies) are listed by 2cm length classes.

Year	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1994	-	-	-	-	-	-	-	<0.1	<0.1	<0.1	0.2	0.4	0.6	0.7	0.8	1.0	1.4	1.9	2.7	3.5	4.0	4.4	4.9	5.5	6.8	7.8	8.0	8.4	8.0	7.1	6.1	4.4	4.0	2.5	1.7	1.2	0.7	0.6	0.2	0.1	<0.1	<0.1	<0.1	<0.1
1995	-	-	-	-	-	-	-	-	-	-	<0.1	<0.1	<0.1	0.2	0.2	0.5	0.9	1.8	2.2	4.4	4.2	5.3	6.4	5.7	7.5	7.1	7.6	8.3	6.2	6.9	6.0	4.8	4.1	3.2	2.8	1.7	0.9	0.6	0.3	0.2	<0.1	<0.1	-	-
1996	-	-	-	-	-	-	-	-	<0.1	<0.1	<0.1	<0.1	0.2	0.3	0.3	0.5	0.8	1.4	2.1	3.2	4.6	5.8	6.5	8.8	8.3	8.3	8.6	7.5	7.1	6.1	5.2	4.1	3.2	2.6	1.6	1.1	0.8	0.4	0.3	0.1	<0.1	<0.1	<0.1	<0.1
1997	-	-	-	-	-	-	-	-	-	-	-	<0.1	0.3	0.3	0.7	1.1	1.5	2.7	2.8	4.6	4.7	4.6	6.0	6.8	7.6	7.2	7.8	7.9	7.0	6.7	5.1	3.9	3.0	2.6	2.4	1.2	0.6	0.4	0.2	<0.1	<0.1	-	-	-

Table 3.5e: South Coast longline catches-at-length (as percentage frequencies), assumed to be *M. capensis* only, are listed by 2cm length classes.

Year	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105
1994	-	-	-	-	-	-	-	-	-	-	<0.1	<0.1	0.2	0.2	0.7	1.2	2.2	3.5	5.5	6.9	8.2	8.2	9.0	8.3	7.9	7.8	6.6	6.0	4.5	3.7	2.6	2.0	1.4	1.1	0.8	0.6	0.4	0.3	<0.1	<0.1	<0.1	<0.1	-	-
1995	-	-	-	-	-	-	-	-	-	-	<0.1	<0.1	<0.1	0.2	0.2	0.5	0.9	1.8	2.2	4.4	4.2	5.3	6.4	5.7	7.5	7.1	7.6	8.3	6.2	6.9	6.0	4.8	4.1	3.2	2.8	1.7	0.9	0.6	0.3	0.2	<0.1	<0.1	-	-
1996	-	-	-	-	-	-	-	-	-	-	-	-	<0.1	0.4	1.1	1.6	3.1	4.3	3.8	4.8	5.6	6.9	7.5	8.7	9.0	9.3	8.9	7.0	5.9	4.5	2.5	2.4	1.3	0.7	0.2	0.3	0.1	<0.1	<0.1	<0.1	-	-	-	-
1997	-	-	-	-	-	-	-	-	-	-	-	<0.1	0.1	0.3	0.5	1.2	1.7	2.7	3.3	4.3	4.4	5.2	6.4	7.6	8.6	8.9	8.8	8.4	7.7	6.6	4.8	3.0	2.3	1.4	0.7	0.4	0.3	0.1	0.1	<0.1	<0.1	-	<0.1	-

Table 3.6a: A break-down of the **state** of stomachs of *M. capensis* and *M. paradoxus* predators by predator length is shown for the **West Coast** (1999-2013 DAFF data set, T. Fairweather, *pers. comm.*). Values in parentheses correspond to percentages of the total for each length class, while all other values are counts. All stomachs that are not empty or everted have been classed as "Full".

	M. capensis													
Stomach state	≤ 20cm		21-30cm		31-40cm		41-50cm		51-60cm		61-70cm		>70cm	
Total	690		1478		1360		1058		1143		930		641	
Full	324	(47)	361	(24)	345	(25)	276	(26)	288	(25)	275	(30)	186	(29)
Empty	282	(41)	967	(65)	795	(58)	503	(48)	552	(48)	422	(45)	259	(40)
Everted	84	(12)	150	(10)	220	(16)	279	(26)	303	(27)	233	(25)	196	(31)
	M. paradoxus													
Stomach state	≤ 20cm		21-30cm		31-40cm		41-50cm		51-60cm		61-70cm		>70cm	
Total	1127		1554		1218		1304		1024		734		515	
Full	440	(39)	299	(19)	201	(17)	165	(13)	111	(11)	73	(10)	50	(10)
Empty	632	(56)	1088	(70)	801	(66)	888	(68)	587	(57)	325	(44)	222	(43)
Everted	55	(5)	167	(11)	216	(18)	251	(19)	326	(32)	336	(46)	243	(47)

Table 3.6b: Repeat of Table 3.6a for the **South Coast**. Data from the South Coast have not been incorporated into the hake predation model presented in this thesis (see text for reasons).

	M. capensis													
Stomach state	≤ 20cm		21-30cm		31-40cm		41-50cm		51-60cm		61-70cm		>70cm	
Total	936		1215		1676		2092		1808		1405		933	
Full	469	(50)	562	(46)	615	(37)	664	(32)	627	(35)	451	(32)	360	(39)
Empty	399	(43)	617	(51)	983	(59)	1218	(58)	836	(46)	618	(44)	337	(36)
Everted	68	(7)	36	(3)	78	(5)	210	(10)	345	(19)	336	(24)	236	(25)
	M. paradoxus													
Stomach state	≤ 20cm		21-30cm		31-40cm		41-50cm		51-60cm		61-70cm		>70cm	
Total	42		331		1268		605		319		253		136	
Full	12	(29)	68	(21)	235	(19)	56	(9)	28	(9)	11	(4)	11	(8)
Empty	26	(62)	215	(65)	822	(65)	393	(65)	177	(55)	132	(52)	59	(43)
Everted	4	(10)	48	(15)	211	(17)	156	(26)	114	(36)	110	(43)	66	(49)

Table 3.7: Break down of prey items found in the stomachs of *M. capensis* and *M. paradoxus* predators on the West Coast and South Coast (1999-2013 DAFF data set, T. Fairweather, *pers. comm.*). Prey items are classified into four main groups: fish (mass-length relationship known), fish (mass-length relationship not known), crustaceans (mainly hard-bodied prey items) and mollucs (mainly soft-bodied prey items). Where possible, common names have been provided in parenthesis. Totals for each group are recorded as number of samples, while the break down within each group is listed as percentage frequencies. A '-' indicates that no samples of the corresponding prey species were found for the given predator. If several prey items of the same species were recorded in a predator's stomach, this has been taken into account in the counts provided below. If the number of prey items of a certain kind in a single stomach sample was not recorded in the database, it is assumed to be one. Note that since total numbers of samples recorded are counts of number of prey items, the totals do not correspond to those in Tables 3.6a and 3.6b, which are counts of the number of predator stomachs sampled.

		M. capensis		*M. paradoxus*	
Fish, mass-length relationship known		West Coast	South Coast	West Coast	South Coast
Total number of samples		1165	2985	158	41
Austroglossus microlepis	(West Coast sole)	0.1	-	-	-
Austroglossus pectoralis	(Mud sole)	-	0.3	-	-
Chelidonichthys	(Gurnard)	-	0.3	-	-
Chelidonichthys capensis	(Cape gurnard)	0.2	-	-	-
Engraulis encrasicolus	(Anchovy)	23.3	45.6	17.7	58.5
Etrumeus whiteheadi	(Redeye roundherring)	11.3	12.6	3.2	7.3
Genypterus capensis	(Kingklip)	0.2	0.2	-	-
Merluccius	(Unidentified hake)	16.1	4.8	26.6	19.5
Merluccius capensis	(Shallow-water hake)	5.7	3.7	-	-
Merluccius paradoxus	(Deep-water hake)	25.3	2.8	49.4	4.9
Sardinops sagax	(Sardine)	0.9	2.5	-	-
Scomber japonicus	(Chub mackerel)	0.1	1.2	-	-
Sufflogobius bibarbatus	(Pelagic goby)	0.4	-	-	-
Trachurus trachurus capensis	(Cape horse mackerel)	16.4	26.0	3.2	9.8
		M. capensis		*M. paradoxus*	
Fish, mass-length relationship not known		West Coast	South Coast	West Coast	South Coast
Total number of samples		902	1326	801	358
Alepes djedaba	(Shrimp scad)	-	1.0	-	4.2
Anguilliformes	(Eel)	0.1	0.4	0.1	-
Argyropelecus	(Hatchetfish)	-	-	0.1	-
Arnoglossus capensis	(Cape scaldfish)	0.1	-	-	-
Astronesthidae	(Snaggletooth)	-	-	-	0.3
Atractoscion aequidens	(Geelbek croaker)	-	0.1	-	-
Avocettina	(Snipe eel)	-	-	0.1	-
Bathophilus longipinnus	(Barbeled dragonfish)	-	-	0.2	-
Brama brama	(Atlantic pomfret)	0.2	-	-	-
Callanthias legras	(Splendid perch)	-	0.3	-	-
Champsodon capensis	(Gaper)	0.1	1.7	-	-
Chauliodus sloani	(Sloane's viperfish)	-	-	0.1	2.8
Chelidonichthys queketti	(Lesser gurnard)	0.1	1.3	-	-
Chlorophthalmus punctatus	(Spotted greeneye)	0.2	-	-	1.1
Coelorinchus	(Rattail)	-	-	0.1	-
Coelorinchus braueri	(Shovelnose grenadier)	-	-	-	-
Coelorinchus simorhynchus	(Rattail)	4.2	0.3	1.2	-
Cubiseps		-	-	-	0.3
Cynoglossus capensis	(Sand tonguesole)	0.2	1.0	-	-
Cynoglossus zanzibarensis	(Respotted tonguesole)	2.7	3.2	0.1	-
Diaphus	(Lanternfish)	-	-	0.6	-
Diaphus hudsoni	(Hudson's lanternfish)	-	-	-	0.3

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Table 3.7: *... continued from previous page*

Emmelichthys nitidus	(Cape bonnetmouth)	3.0	-	-	-
Epigonus	(Cardinalfish)	0.3	-	0.4	-
Epigonus denticulatus	(Pencil cardinalfish)	0.3	-	0.2	-
Gnathophis	(Congrid eel)	2.7	5.7	0.1	0.6
Gobiidae	(Goby)	1.7	-	-	-
Gonorhynchus gonorhynchus	(Beaked salmon)	0.3	0.5	-	-
Helicolenus dactylopterus	(Blackbelly rosefish)	3.2	1.4	0.4	0.8
Lampadena	(Lanternfish)	-	-	0.2	-
Lampanyctodes hectoris	(Hector's lanternfish)	12.3	-	24.3	2.0
Lampanyctus	(Lanternfish)	-	-	0.1	-
Lepidion capensis		0.1	-	-	-
Lepidopus caudatus	(Silver scabbardfish)	2.3	1.5	-	-
Lophius vomerinus	(Devil anglerfish)	-	0.1	-	-
Lucigadus ori	(Bronze whiptail)	-	-	0.1	-
Malacocephalus laevis	(Softhead grenadier)	0.1	-	-	-
Malacosteidae	(Loosejaw)	-	-	-	0.3
Malacosteus niger	(Stoplight loosejaw)	-	-	0.2	-
Maurolicus walvisensis	(ex *muelleri*)	6.4	-	19.7	23.5
Melamphaidae	(Ridgehead)	-	-	-	-
Myctophidae	(Lanternfish)	1.8	1.9	5.9	27.4
Neoscopelus macrolepidotus	(Large-scaled lanternfish)	-	-	0.1	-
Nezumia	(Rattail)	-	-	0.1	-
Notacanthus sexspinis	(Spiny-back eel)	-	-	-	-
Paracallionymus costatus	(Ladder dragonet)	21.1	9.1	4.5	5.0
Paralepididae	(Barracudina)	-	-	0.1	-
Peristedion weberi	(Armored searobin)	-	-	-	0.3
Photichthyidae	(Lightfish)	-	-	0.6	-
Photichthys argenteus	(Silver lightfish)	-	-	0.6	0.8
Physiculus capensis	(Bigeye rockling)	0.1	-	-	-
Pleuronectiformes	(Flatfish)	-	0.2	-	-
Pomatomus saltatrix	(Bluefish)	-	0.1	-	-
Pterogymnus laniarius	(Panga seabream)	-	0.4	-	-
Rhabdosargus globiceps	(White stumpnose)	-	0.2	-	-
Scopelosaurus	(Waryfish)	-	-	-	0.3
Scopelosaurus meadi	(Blackring waryfish)	-	-	0.1	-
Spicara axillaris		-	0.2	-	-
Stomias boa	(Scaly dragonfish)	-	-	0.1	-
Strongylura leiura	(Banded needlefish)	-	0.2	-	-
Symbolophorus	(Lanternfish)	-	-	2.2	2.2
Symbolophorus barnardi	(Barnard's lanternfish)	-	-	-	1.4
Symbolophorus boops	(Bogue lanternfish)	-	-	2.0	5.3
Synagrops japonicus		-	-	-	0.3
Syngnathidae	(Blackmouth splitfin)	-	0.3	-	-
Teleostei	(Fish)	0.8	2.2	0.6	0.6
Teleostei demersal	(Demersal fish)	4.5	2.9	5.0	0.8
Teleostei pelagic	(Pelagic fish)	10.6	27.4	10.4	3.6
Thyrsites atun	(Snoek)	-	0.1	-	-
Tripterophysis gilchristi		-	0.1	-	-
Ostraciidae	(Trunkfish)	0.1	-	-	-
Unid Fish	(Unidentified fish)	20.1	36.0	18.7	15.9
Zeus capensis	(Cape dory)	0.1	0.4	-	-

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Table 3.7: *... continued from previous page*

		M. capensis		*M. paradoxus*	
Crustaceans		West Coast	South Coast	West Coast	South Coast
Total number of samples		2131	1570	1898	1384
Amphipoda	(Amphipod)	36.6	3.2	26.6	0.2
Brachyrhncha	(Crab)	0.1	-	-	-
Caridea	(Caridean shrimp)	0.8	2.5	1.2	0.9
Copepoda	(Copepod)	0.1	7.3	4.5	0.1
Crustacea	(Crustacean)	0.8	3.7	0.5	0.7
Decapoda	(Decapod)	-	0.1	-	-
Euphausiidae	(Krill)	40.5	31.7	54.9	94.6
Funchalia	(Prawn)	1.9	0.4	0.9	-
Funchalia woodwardi	(Prawn)	3.9	8.2	3.6	1.2
Isopoda	(Crustacean)	0.4	0.1	0.6	-
Jasus lalandi	(West Coast rock lobster)	-	-	0.1	-
Mursia cristiata	(Crab)	-	0.1	-	0.1
Mysiidae		0.1	1.5	0.7	0.1
Natantia	(Crustacean)	6.1	20.2	5.0	2.0
Paguridae	(Hermit crab)	-	0.6	-	-
Pasiphaea		5.6	0.1	0.7	-
Penaeidae	(Penaed shrimp)	0.3	0.2	0.6	-
Pterosquilla capensis		2.7	20.2	0.2	-
Sergesters laminates		-	-	-	0.1
Shell		0.1	-	-	-
Solenocera	(Shrimp)	-	0.1	-	-
Solenocera africana	(African mud shrimp)	-	-	-	-
		M. capensis		*M. paradoxus*	
Molluscs		West Coast	South Coast	West Coast	South Coast
Total number of samples		168	303	103	87
Abraliopsis gilchristi		-	-	1.9	-
Argonauta	(Pelagic octopus)	-	0.3	-	-
Asteroidea	(Starfish)	-	0.3	-	-
Austrorossia enigmatica	(Bobtail squid)	1.8	-	1.9	-
Cephalopoda	(Cephalopod)	7.1	5.0	21.4	26.4
Echinodermata	(Echinoderm)	-	0.7	-	-
Echinoidea	(Sea urchin)	-	-	-	-
Fasciolaria	(Tulip snail)	-	0.3	-	-
Fasciolaridae		-	0.7	-	-
Gastropoda	(Snail)	-	0.3	-	-
Histioteuthis	(Squid)	-	-	1.9	2.3
Holothuroidea	(Sea cucumber)	-	1.0	-	-
Loligo reynaudii	(Cape Hope squid)	1.8	17.8	1.0	2.3
Lolliguncula mercatoris		3.0	0.3	-	-
Lycoteuthis lorigera	(Squid)	-	-	14.6	27.6
Marginella musica	(Margin snail)	0.6	-	-	-
Megalopae larvae	(Crab Larvae)	-	0.3	-	-
Mollusca	(Mollusc)	-	0.3	-	-
Onychoteuthis	(Clubhook squid)	-	-	1.0	-
Sepia	(Cuttlefish)	15.5	28.1	1.0	2.3
Sepia australis	(Southern cuttlefish)	35.1	22.8	1.9	1.1
Sepia hieronis		0.6	0.3	-	-
Teleostei larva	(Fish larva*)	-	-	1.0	-
Teuthoidea		-	-	1.0	-
Todarodes	(Japanese flying squid)	0.6	-	1.0	-
Todarodes angolensis	(Angola flying squid)	-	0.3	1.9	-
Todaropsis eblanae	(Lesser flying squid)	33.9	21.1	48.5	37.9

**Included under "molluscs" given that these comprise soft body parts*

Table 3.8a: A break-down of prey items found in the stomachs of *M. capensis* and *M. paradoxus* predators by **prey type** (fish, crustacean and mollusc) and predator length for the **West Coast** (1999-2013 DAFF data set, T. Fairweather, *pers. comm.*). Note that since these are counts of number of prey items, the totals do not correspond to those in Table 3.6a, which are counts of the number of predator stomachs sampled.

(i) *M. capensis*							
Prey type	≤20cm	20-30	30-40	40-50	50-60	60-70	≥ 70cm
Merluccius capensis	2	13	16	8	10	5	12
Merluccius paradoxus	0	7	19	41	89	86	53
Merluccius	1	11	16	35	58	43	24
Other fish	92	259	314	260	253	208	132
Total fish prey	95	290	365	344	410	342	221
Crustaceans	695	968	200	150	59	38	21
Molluscs	1	13	45	25	33	32	19
Total	791	1271	610	519	502	412	261
(ii) *M. paradoxus*							
Prey type	≤20cm	20-30	30-40	40-50	50-60	60-70	≥ 70cm
Merluccius capensis	0	0	0	0	0	0	0
Merluccius paradoxus	0	1	3	7	16	25	26
Merluccius	0	1	1	7	15	8	10
Other fish	219	230	171	109	58	35	17
Total fish prey	219	232	175	123	89	68	53
Crustaceans	570	528	589	109	60	35	7
Molluscs	1	4	24	37	17	16	4
Total	790	764	788	269	166	119	64

Table 3.8b: Repeat of Table 3.8a for the **South Coast**. Data from the South Coast have not been incorporated into the hake predation model presented in this thesis, for reasons given in the text.

(i) *M. capensis*							
Prey type	≤20cm	20-30	30-40	40-50	50-60	60-70	≥ 70cm
Merluccius capensis	1	5	8	9	26	27	35
Merluccius paradoxus	0	0	0	2	26	34	21
Merluccius	2	9	5	10	27	40	51
Other fish	208	603	726	815	773	509	339
Total fish prey	211	617	739	836	852	610	446
Crustaceans	548	68	216	225	319	134	60
Molluscs	24	17	33	43	64	98	24
Total	783	702	988	1104	1235	842	530
(ii) *M. paradoxus*							
Prey type	≤20cm	20-30	30-40	40-50	50-60	60-70	≥ 70cm
Merluccius capensis	0	0	0	0	0	0	0
Merluccius paradoxus	0	0	0	0	0	1	1
Merluccius	0	1	3	1	0	1	2
Other fish	0	93	183	49	36	13	15
Total fish prey	0	94	186	50	36	15	18
Crustaceans	20	503	714	140	6	0	1
Molluscs	0	2	44	20	12	3	6
Total	20	599	944	210	54	18	25

Table 3.9: Counts of numbers of hake prey in the stomachs of hake predators are listed by predator and prey species and age combinations. These counts have been converted from the counts by predator and prey lengths from the 1999-2013 DAFF data set (T. Fairweather, *pers. comm.*) by calculating the expected ages from the von Bertalanffy growth curve for hake. Note that these data are for the West Coast only and have been aggregated over the years 1999-2013.

		Prey age									
		0	1	2	3	4	5	6	7	8	9
M. capensis predators, *M. capensis* prey											
Predator age	1	7									
	2	12	0								
	3	3	7	0							
	4	1	3	0	0						
	5	1	7	1	0	0					
	6	1	3	0	1	0	0				
	7	0	2	1	1	0	0	0			
	8	0	0	0	0	0	0	0	0		
	9	0	0	0	0	1	0	0	0	0	
	10	0	0	0	0	0	0	0	0	0	0
M. capensis predators, *M. paradoxus* prey											
Predator age	1	6									
	2	7	1								
	3	15	3	0							
	4	17	25	2	0						
	5	16	42	0	0	0					
	6	4	41	6	2	0	0				
	7	1	17	8	2	0	0	0			
	8	0	7	2	2	2	0	0	0		
	9	0	2	0	0	0	0	0	0	0	
	10	0	0	0	0	0	0	0	0	0	0
M. paradoxus predators, *M. paradoxus* prey											
Predator age	1	0									
	2	1	0								
	3	2	2	0							
	4	3	7	0	0						
	5	4	12	1	0	0					
	6	1	4	3	0	0	0				
	7	0	8	4	0	0	0	0			
	8	1	4	4	1	0	0	0	0		
	9	0	0	0	0	0	0	0	0	0	
	10	0	0	1	0	0	0	0	0	0	0

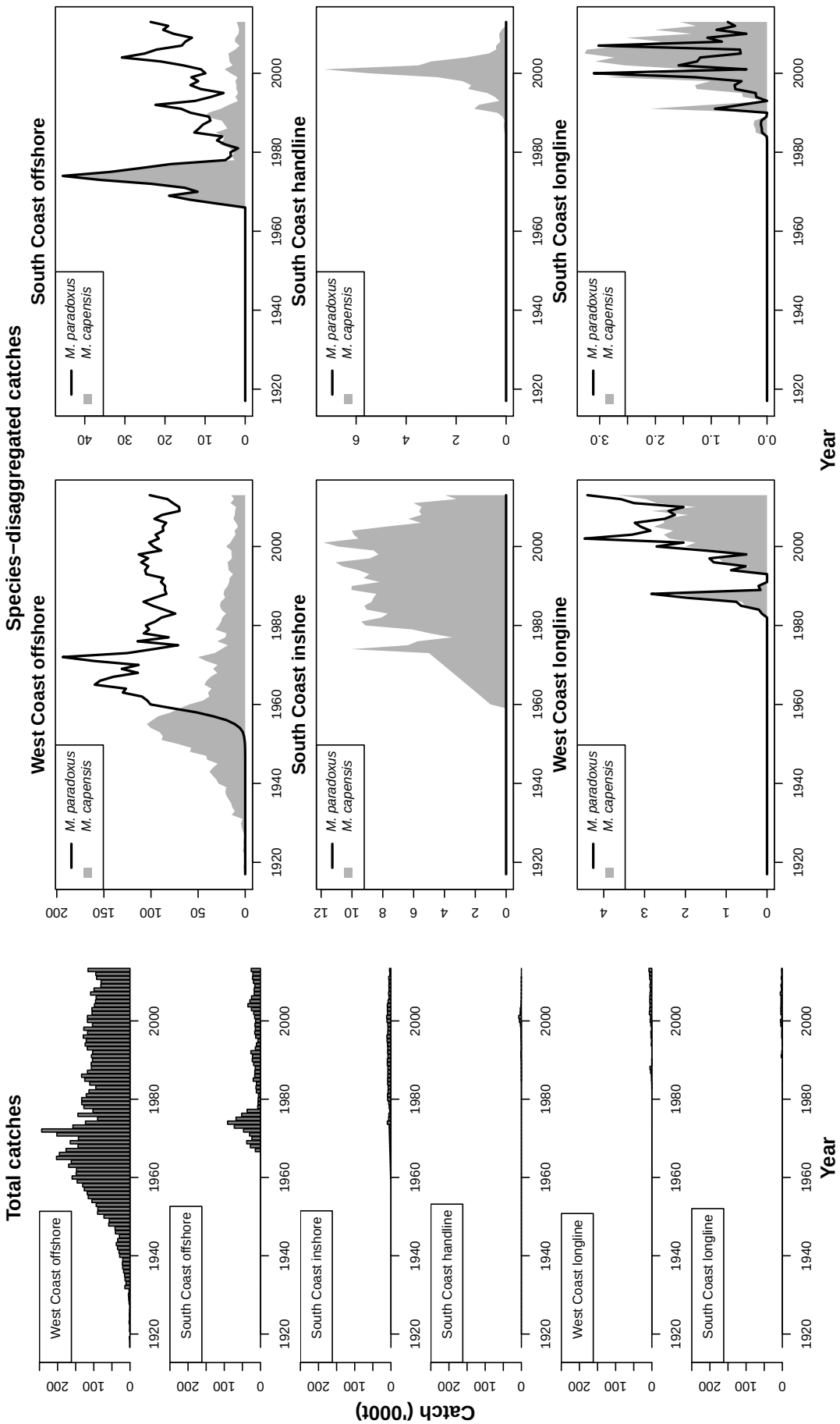

Figure 3.1: The leftmost panel shows the total species-aggregated annual catches for each fishing fleet, illustrating the varying magnitudes of catch among the different sectors. The species-disaggregated catches are shown in the centre and rightmost panels, with *M. capensis* catches indicated by the grey shaded area, and the *M. paradoxus* catches by the solid black line. Note that while the plots in the leftmost panel all have the same vertical scale, this scale changes for the other sets of panels to provide improved contrast.

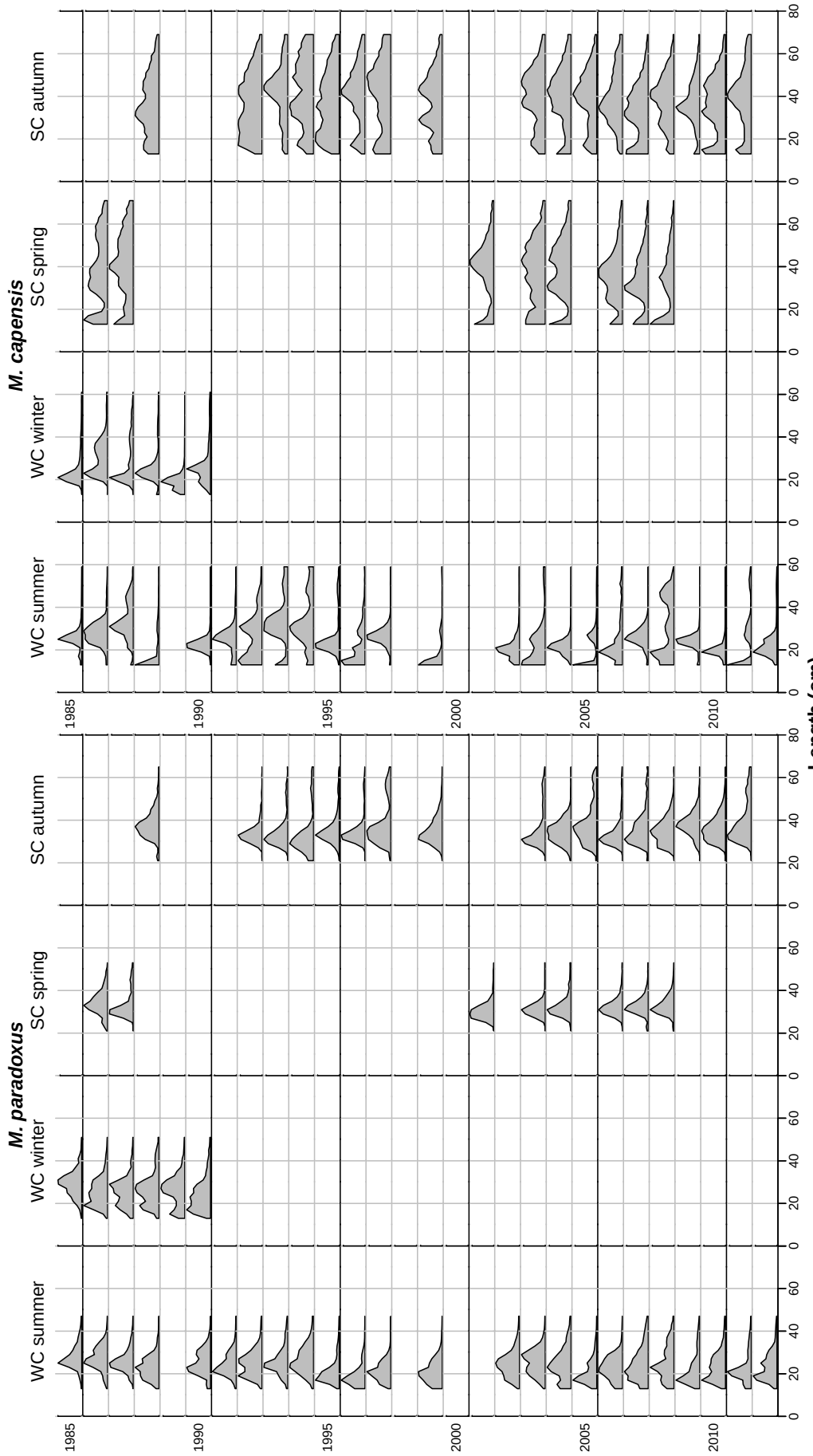

Figure 3.2: Plots of the hake proportions-at-length from the surveys, for each species and survey.

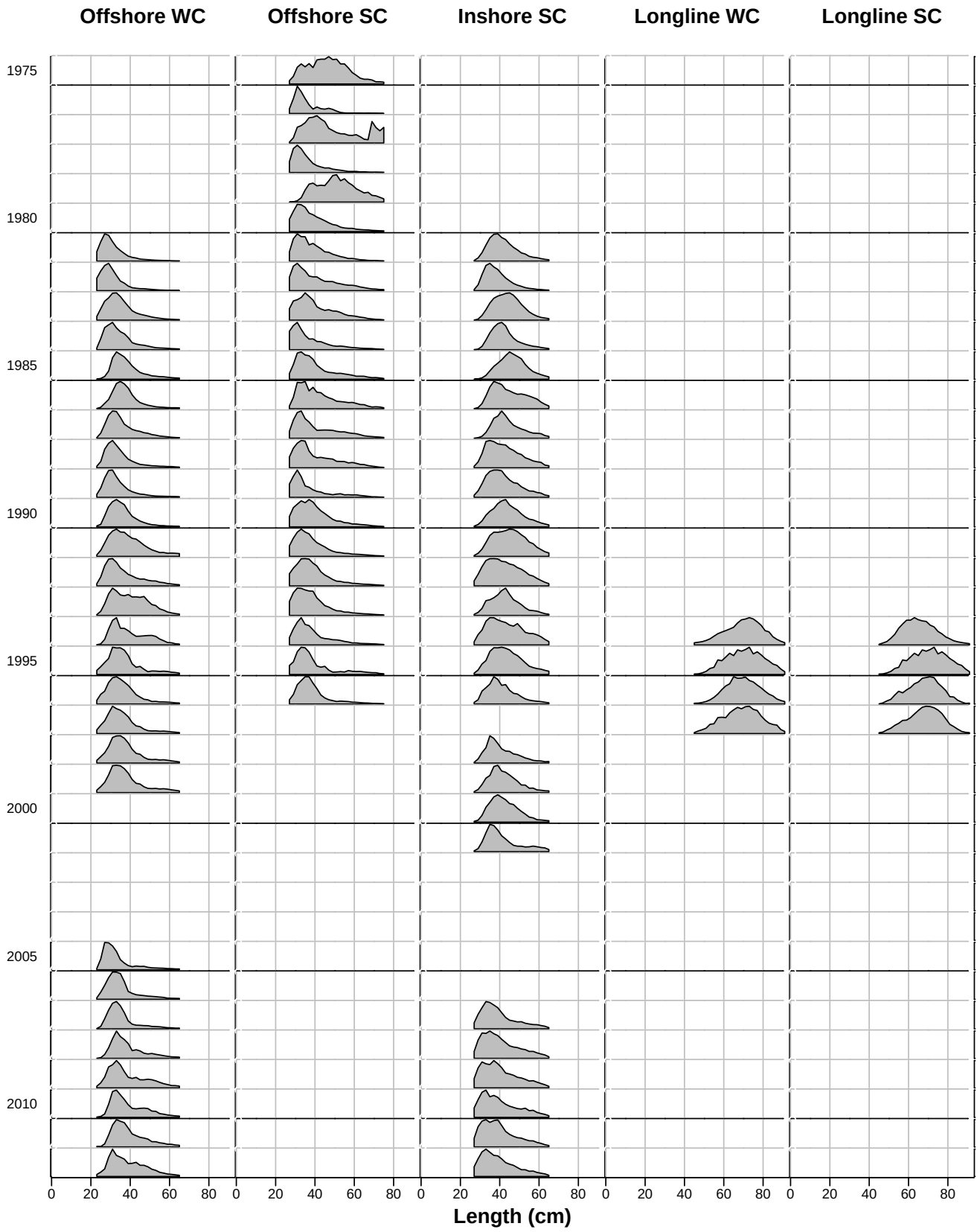

Figure 3.3: Plots of the hake commercial catches-at-length by year and fishing fleet.

Appendices

3.A Investigating different methods for obtaining hake survey probability distributions for length, and an inspection of the sub-sample for which biological information was measured

Special thanks go to T. P. Fairweather for her input on sampling and data-analysis procedures and to R. A. Rademeyer for re-running her hake model with the updated catch-at-length dataset to contribute to the information and results presented below.

3.A.1 Introduction

The investigation that gave rise to this appendix was instigated to assess the sampling strategy used to obtain the diet data, in order to ascertain whether that sampling strategy might be giving rise to biases in the estimates for the population as a whole in terms of both the length distributions and the proportions of hake in the diet of hake predators. This required an examination of the raw survey catch-at-length data and the methods used to analyse these data, and resulted in a few suggestions being made for alternative approaches to weighting the length probability distributions from individual trawls in order to obtain aggregated distributions for each stratum.

This appendix gives the details of the survey sampling procedures, the equations for the methodology currently in place for calculating probability distributions for length, as well as equations for suggested alternative methods for weighting. Figures illustrating the impact that these alternative methods have on the probability distributions for length are provided.

A further aspect of this appendix is an inspection of the sub-sample of the survey catch for which biological parameters are measured, in order to assess the sampling strategy for obtaining biological information and whether the biological samples collected may be considered a reasonable representation of the population.

3.A.2 Survey sampling procedure

Note that the survey sampling procedure has already been described in the main text of this chapter, but has been repeated here for the reader's ease.

Each cruise consists of a series of individual trawls conducted at different stations. The sampling procedure followed for each trawl is as follows.

1. Generally, all small (<16cm) and large (>40-45cm) fish are sorted by species and measured individually for length.
2. Fish between 16cm and 45cm often form the bulk of the catch and will generally be sub-sampled:
   (a) Since there will be an inclination to pick larger fish first, all the hake are sorted by species and into bins of two size categories: "large" and "small" (these terms are relative within a catch). For some surveys, there are a further two categories for sex, i.e large male, small male, large female, small female. All the bins in each category are weighed individually and noted against the relevant category, but only the total weight is captured in the database.

(b) Bins are selected at random from the sorted bins to ensure all fish sizes are measured for length. These are referred to as the 'observed' measures. Since larger hake occur less frequently in the catch, in practice this means that generally all bins containing larger hake are measured, and only some of the bins containing smaller hake are measured.

3. Thus for every category of hake in the catch there will be a catch weight (the sum of the weight of all the bins) and a sample or 'observed' weight (the sum of the weight of the bins measured). Note that the fish that are measured individually for length are not weighed individually; only a combined mass is recorded. This is largely because conditions at sea do not allow for a high degree of accuracy when weighing individually.

3.A.3 A note on nomenclature

In the chapter describing the hake predation model (Chapter 5), the superscripts s_p and l_p are used for species and length of hake predators, while the subscripts s and l are used for hake prey. Thus, in the interest of compatibility with documentation of the predation model, the superscripts s_p and l_p have been used for species and length of hake caught in the survey, as these hake represent the predators in the predation model.

3.A.4 Obtaining probability distributions for length from the sample

For years in which there is no sex information available, there are three possible categories for the hake samples: large (L), small (S) and all hake not sorted by size (A).

Let $n_{y,d,t}^{s_p,l_p,i}$ be the number of hake of species s_p in length-group l_p that were measured ('observed') in category i for trawl t in depth stratum d in year y, where $i \in \{L, S, A\}$. The total numbers estimated to have been caught in category i are obtained by scaling the measured numbers up by a ratio of $W_{y,d,t}^{s_p,i}/\widetilde{W}_{y,d,t}^{s_p,i}$, where $W_{y,d,t}^{s_p,i}$ is the total weight of the catch of category i for trawl t in depth stratum d, and $\widetilde{W}_{y,d,t}^{s_p,i}$ is the corresponding weight of the sub-sample of category i that was measured. The total estimated number of hake of length group l_p caught in trawl t and depth stratum d is then:

$$C_{y,d,t}^{s_p,l_p} = n_{y,d,t,l}^{s_p,L} \frac{W_{y,d,t}^{s_p,L}}{\widetilde{W}_{y,d,t}^{s_p,L}} + n_{y,d,t,l}^{s_p,S} \frac{W_{y,d,t}^{s_p,S}}{\widetilde{W}_{y,d,t}^{s_p,S}} + n_{y,d,t,l}^{s_p,A} \frac{W_{y,d,t}^{s_p,A}}{\widetilde{W}_{y,d,t}^{s_p,A}} \tag{3.A.1}$$

The proportion of hake in trawl t and depth stratum d that are of length group l_p is given by:

$$p_{y,d,t}^{s_p,l_p} = \frac{C_{y,d,t}^{s_p,l_p}}{\sum_{l_p} C_{y,d,t}^{s_p,l_p}} \tag{3.A.2}$$

The probability distribution for length for depth stratum d is obtained from a weighted average of the probability distributions for length from the individual trawls in that depth stratum:

$$p_{y,d}^{s_p,l_p} = \frac{\sum_t \alpha_{y,d,t}^{s_p} p_{y,d,t}^{s_p,l_p}}{\sum_t \alpha_{y,d,t}^{s_p}} \tag{3.A.3}$$

The weighting factor α_t is defined as follows:

$$\alpha_{y,d,t}^{s_p} = \begin{cases} 100 & \text{for } n_{y,d,t}^{s_p} > 100 \\ n_{y,d,t}^{s_p} & \text{for } n_{y,d,t}^{s_p} \leq 100 \end{cases} \tag{3.A.4}$$

where $n_{y,d,t}^{s_p} = \sum_{i=L,S,A} \sum_l n_{y,d,t}^{s_p,l_p,i}$ is the total number of hake measured in trawl t in depth stratum d. This approach is a consequence of the assumption that the hake population is distributed homogeneously across depth stratum d and each trawl represents a random sample from that depth stratum. In line with this assumption, all trawls should receive the same weighting unless the sample size is very small. In reality, however, the hake population is not homogeneously distributed, so that it could be argued that the density of the hake population at the location of each trawl should be taken into account. In other words:

$$p_{y,d}^{s_p,l_p} = \frac{\sum_t \widetilde{\alpha}_{y,d,t}^{s_p} p_{y,d,t}^{s_p,l_p}}{\sum_t \widetilde{\alpha}_{y,d,t}^{s_p}} \tag{3.A.5}$$

where $\widetilde{\alpha}_{y,d,t}^{s_p} = \alpha_{y,d,t}^{s_p} \beta_{y,d,t}^{s_p}$, with $\alpha_{y,d,t}^{s_p}$ being as in Equation 3.A.4 above, and $\beta_{y,d,t}^{s_p}$ being a measure of density for trawl t, calculated by dividing the total number of hake of species s_p estimated to have been caught in the trawl by the area swept by the trawl, i.e.:

$$\beta_{y,d,t}^{s_p} = \frac{\sum_l C_{y,d,t}^{s_p,l_p}}{A_{y,d,t}} \tag{3.A.6}$$

This appendix explores the impact of weighting without density (Equation 3.A.3) compared to weighting with density (Equation 3.A.5) on the resulting probability distributions for length. The appendix further investigates the effect of the choice of 100 as the sample size above which sampling variability is assumed to no longer dominate (Equation 3.A.4). Given:

$$\alpha_{y,d,t}^{s_p} = \begin{cases} X & \text{for } n_{y,d,t}^{s_p} > X \\ n_{y,d,t}^{s_p} & \text{for } n_{y,d,t}^{s_p} \leq X \end{cases} \tag{3.A.7}$$

values $X \in \{50, 100, 200\}$ are explored.

Results are presented at both stratum-disaggregated and stratum-aggregated levels. In order to obtain a stratum-aggregated probability distribution for length, the probability distributions for length from each stratum are weighted according to the estimated population size (in numbers) in that depth stratum, i.e.:

$$p_y^{s_p,l_p} = \frac{\sum_d N_{y,d}^{s_p} p_{y,d}^{s_p,l_p}}{\sum_d N_{y,d}^{s_p}} \tag{3.A.8}$$

For results shown in this appendix, the survey estimated population size $N_{y,d}^{s_p}$ has been calculated in two ways, which, along with taking density-weighting into account, was followed by the Rademeyer and Butterworth (2014b) hake model being re-run for three different cases.

Reference Case (RC): Density-weigthing **is not** taken into account, and $\mathbf{N_{y,d}^{s_p}} = \mathbf{B_{y,d}^{s_p,surv}} / \mathbf{\bar{W}_{y,d}^{s_p}}$, where $B_{y,d}^{s_p,surv}$ is the survey biomass estimate for stratum d in year y and $\bar{W}_{y,d}^{s_p}$ is the mean weight of hake

for stratum d in year y given by $\bar{W}^{s_p}_{y,d} = \sum_{l_p} p^{s_p,l_p}_{y,d} \alpha (l_p)^{\beta}$. The parameters α and β are the weight-length parameters for hake. This is the method that is currently in use.

Sensitivity 1 (Sen1): Density-weighting **is not** taken into account, and $\mathbf{N^{s_p}_{y,d}}$ **is calculated from the survey samples directly** by averaging the densities for each trawl across stratum d to obtain an average density for the stratum (i.e. $\sum_t \beta^{s_p}_{y,d,t} / \sum_t 1$), and multiplying this average by the total area of the stratum.

Sensitivity 2 (Sen2): Density-weighting **is** taken into account, and $\mathbf{N^{s_p}_{y,d}}$ **is calculated from the survey samples directly** by averaging the densities for each trawl across stratum d to obtain an average density for the stratum (i.e. $\sum_t \beta^{s_p}_{y,d,t} / \sum_t 1$), and multiplying this average by the total area of the stratum.

3.A.5 Obtaining sex-disaggregated proportions

In certain years, a sub-sample of the measured catch was also sexed. Let $n^{s_p,l_p,i}_{g,y,d,t}$ be number of hake of species s_p, gender g and length group l_p measured in category i ($i \in \{L, S, A\}$) of trawl t in depth stratum d. Then the total number of hake of gender g and length group l_p estimated to have been caught in trawl t and depth stratum d is then:

$$C^{s_p,l_p}_{g,y,d,t} = n^{s_p,L}_{y,g,d,t} \frac{W^{s_p,L}_{g,y,d,t}}{\widetilde{W}^{s_p,L}_{g,y,d,t}} + n^{s_p,S}_{y,g,d,t} \frac{W^{s_p,S}_{g,y,d,t}}{\widetilde{W}^{s_p,S}_{g,y,d,t}} + n^{s_p,A}_{y,g,d,t} \frac{W^{s_p,A}_{g,y,d,t}}{\widetilde{W}^{s_p,A}_{g,y,d,t}} \tag{3.A.9}$$

$W^{s_p,i}_{g,y,d,t}$ is the total weight of hake of species s_p and gender g caught in category i for trawl t in depth stratum d, and $\widetilde{W}^{s_p,i}_{g,y,d,t}$ is the corresponding weight of the sub-sample of category i that was measured. The total number of hake of gender g of length group l_p estimated to have been caught in stratum d is:

$$C^{s_p,l_p}_{g,y,d} = \sum_t C^{s_p,l_p}_{g,y,d,t} \tag{3.A.10}$$

The proportion of the total sexed catch in length group l_p that is of gender g is calculated by:

$$q^{s_p,l_p}_{g,y,d} = \frac{C^{s_p,l_p}_{g,y,d}}{\sum_{g'} C_{g',d,l}} \tag{3.A.11}$$

Strictly speaking, however, the $q^{s_p,l_p}_{g,y,d}$ values should be weighted as in Equation 3.A.3. For the results presented in this document, the following approach was taken.

Define a trawl-specific $q^{s_p,l_p}_{g,y,d,t}$:

$$q^{s_p,l_p}_{g,y,d,t} = \frac{C^{s_p,l_p}_{g,y,d,t}}{\sum_{g'} C^{s_p,l_p}_{g',y,d,t}} \tag{3.A.12}$$

The $q^{s_p,l_p}_{g,y,d}$ for stratum d is then given by:

$$q^{s_p,l_p}_{g,y,d} = \frac{\sum_t \widetilde{\alpha}^{s_p,\text{sexed}}_{y,d,t} q^{s_p,l_p}_{g,y,d,t}}{\sum_t \widetilde{\alpha}^{s_p,\text{sexed}}_{y,d,t}} \tag{3.A.13}$$

where $\widetilde{\alpha}^{s_p,\text{sexed}}_{y,d,t} = \alpha^{s_p,\text{sexed}}_{y,d,t} \beta^{s_p}_{y,d,t}$, similar to Equation 3.A.5, except that:

$$\alpha^{s_p,\text{sexed}}_{y,d,t} = \begin{cases} 100 & \text{for } n^{s_p,\text{sexed}}_{y,d,t} > 100 \\ n^{s_p,\text{sexed}}_{y,d,t} & \text{for } n^{s_p,\text{sexed}}_{y,d,t} \leq 100 \end{cases} \tag{3.A.14}$$

where $n_{y,d,t}^{s_p,\text{sexed}} = \sum_{i=L,S,A} \sum_g \sum_l n_{g,y,d,t}^{s_p,l_p,i}$ is the total number of hake that were sexed and measured in trawl t in depth stratum d. $\beta_{y,d,t}^{s_p}$ is a measure of density for trawl t same as before.

This proportion $q_{g,y,d}^{s_p,l_p}$ is then used to split the proportion-at-length probability distribution $p_{y,d}^{s_p,l_p}$ from Equation 3.A.3 (or 3.A.5) into male and female proportions as follows (taken from Rademeyer 2012).

1. The proportions-at-length are grouped into 2cm length classes.
2. For all length classes < 21cm, the hake are assumed to be juvenile and the proportions-at-length unsexed (U).
3. For length classes ≥ 21cm:

   - If there is sex-information for both of the two 1cm length classes to group (i.e. if $\sum_g q_{g,y,d}^{s_p,l_p} = 1$ and $\sum_g q_{y,g,d}^{s_p,l_p+1} = 1$), then the sex-information is used directly:

$$p_{g,y,d}^{s_p,l_p} = \begin{cases} 0 & \text{for } g = U \\ q_{g,y,d}^{s_p,l_p} p_{y,d}^{s_p,l_p} + q_{y,g,d}^{s_p,l_p+1} p_{y,d}^{s_p,l_p+1} & \text{for } g \in \{M, F\} \end{cases} \tag{3.A.15}$$

   - If there is sex-information for only one of the two 1cm length classes to group (i.e. if $\sum_g q_{g,y,d}^{s_p,l_p} = 1$ or $\sum_g q_{y,g,d}^{s_p,l_p+1} = 1$), then the sex-information from the one length class is used for both:

$$p_{g,y,d}^{s_p,l_p} = \begin{cases} 0 & \text{for } g = U \\ q_{g,y,d}^{s_p,l_p} \left(p_{y,d}^{s_p,l_p} + p_{y,d}^{s_p,l_p+1} \right) \text{ or } q_{y,g,d}^{s_p,l_p+1} \left(p_{y,d}^{s_p,l_p} + p_{y,d}^{s_p,l_p+1} \right) & \text{for } g \in \{M, F\} \end{cases} \tag{3.A.16}$$

   - If there is no sex-information for either of the two 1cm length classes to group (i.e. $\sum_g q_{g,y,d}^{s_p,l_p} = 0$ and $\sum_g q_{y,g,d}^{s_p,l_p+1} = 0$), then the proportion for the resulting 2cm length class is assumed to be unsexed:

$$p_{g,y,d}^{s_p,l_p} = \begin{cases} p_{y,d}^{s_p,l_p} + p_{y,d}^{s_p,l_p+1} & \text{for } g = U \\ 0 & \text{for } g \in \{M, F\} \end{cases} \tag{3.A.17}$$

4. Once the stratum-aggregated $p_{g,y}^{s_p,l_p}$ has been computed (see Equation 3.A.18), then for each 2cm length class of $p_{g,y}^{s_p,l_p}$ greater than 21cm, the male to female ratio for that length class is used to split the unsexed proportion into males and females. If there is no sex information for the length class, then the average of the length classes immediately before and after is used to allocate the unsexed proportion.

The stratum-aggregated $p_{g,y}^{s_p,l_p}$, is calculated in a similar manner to Equation 3.A.8:

$$p_{g,y}^{s_p,l_p} = \frac{\sum_d N_{y,d}^{s_p} p_{g,y,d}^{s_p,l_p}}{\sum_d N_{y,d}^{s_p}} \tag{3.A.18}$$

Here, $N_{y,d}^{s_p}$ is also calculated in two ways according to the methods described in Sen1 and Sen2.

3.A.6 Biological sampling procedure

As for the survey sampling procedure, the biological sampling procedure has already been described in the main text of this chapter, but has been retained here for the reader's ease.

In earlier years, the instructions to scientists undertaking sampling were to collect five specimens per length class for biological sampling (primary target was otolith samples). These samples could be collected across the depth strata. Since smaller hake are encountered more easily (relative abundance and availability to the survey) in waters < 300m, the focus of biological sampling at greater depths is generally on larger hake in order to reach the sampling target. Since the mid-2000s, the minimum number of samples required per length class has been roughly doubled, and the target per length bin is reset for the second half of the cruise.

3.A.7 Results

Note that for all the results presented in this appendix, samples taken at depths greater than 500m have been excluded, since the 501-1000m depth stratum was not sampled consistently throughout the sampling period. Further, in order to help reduce the number of plots, *M. paradoxus* results for the 0-100m depth stratum and *M. capensis* results for the 401-500m depth stratum have not been shown here, since the sample sizes from these depth strata are relatively small.

It can be seen from Figures 3.A.1, 3.A.2 and 3.A.5 that different choices for X (the sample size above which sampling variability is assumed to no longer dominate) make no appreciable difference to the probability distributions. Figures 3.A.3 and 3.A.4, as well as the stratum-aggregated plots in Figures 3.A.6 and 3.A.7, suggest that the impact of weighting by stratum density might be more substantial.

Figures 3.A.8, 3.A.9, 3.A.10 and 3.A.11 superimpose the probability-at-length distributions from the biological samples on top of those from the whole survey sample. The last panel in each plot shows the stratum-aggregated proportions. While the length distributions from the biological samples are rarely an accurate reflection of the length distribution of the population as indicated by the survey (likely as a consequence of the biological sampling strategy), the biological samples do seem to at least represent most length classes reasonably well when aggregated across the depth strata.

Figures 3.A.12 and 3.A.13 show the survey-estimated densities for each stratum and each cruise against the proportion of biological samples taken in each stratum. There seems to be a general trend of a relatively large proportion of biological samples coming from deeper strata where the survey estimates of the population density are small. This is particularly the case for *M. capensis* . This indicates that weighting the diet data by stratum density is justified.

Figure 3.A.14 shows the *M. paradoxus* and *M. capensis* spawning biomass trajectories for the RC, Sen1 and Sen2 approaches to calculating the catches-at-length. The effect of stratum-density weighting on the trajectories seems to be minimal; nevertheless it was considered that the catch-at-length proportions and diet-related quantities from the survey data are less likely to be biased when taking the stratum density where the samples were collected into account.

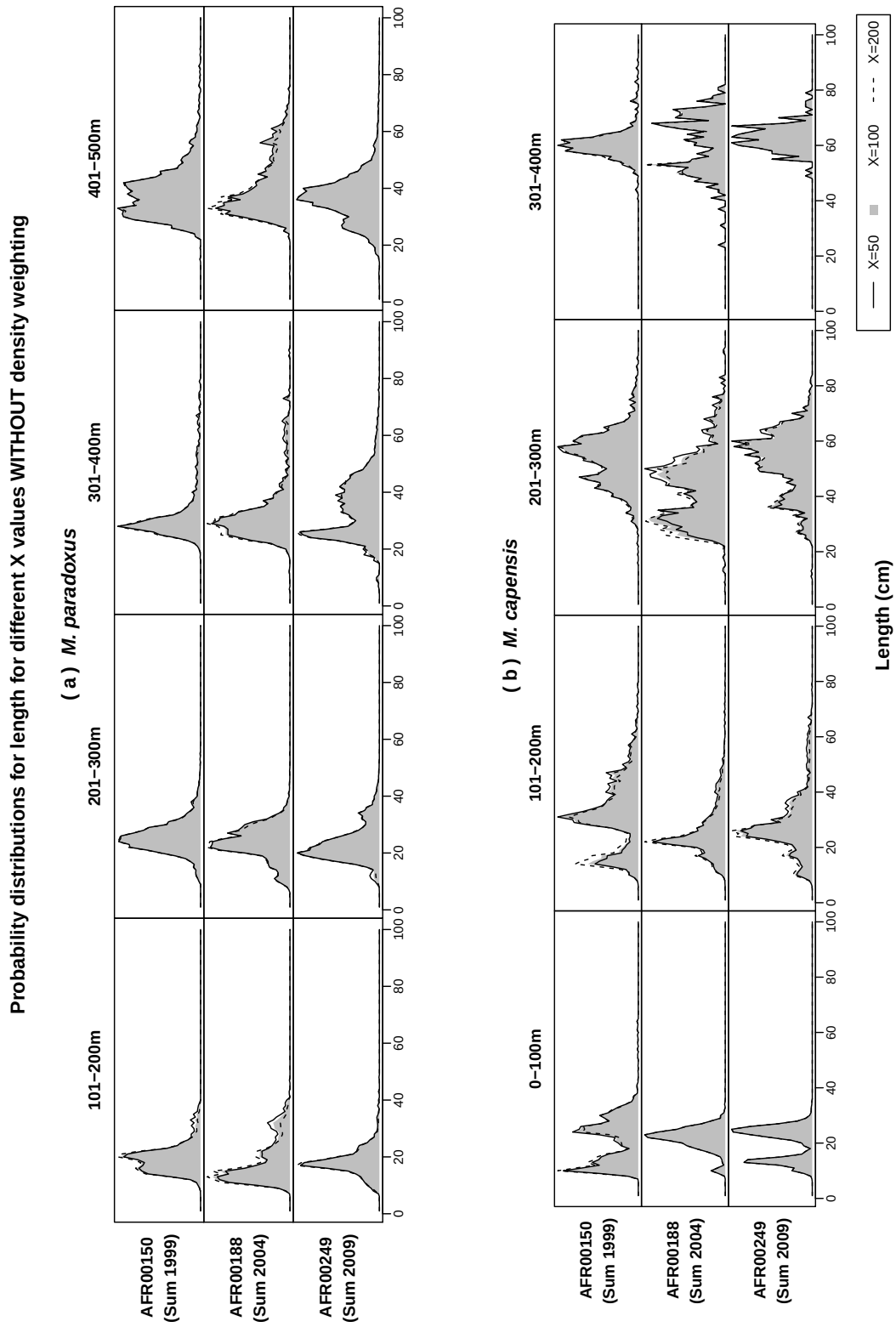

Figure 3.A.1: *M. paradoxus* and *M. capensis* probability distributions for length shown for a selection of three cruises and for three different values of X, the sample size above which sampling variability is assumed to no longer dominate. The results here are for the case when **density weighting is not taken into account** (Equation 3.A.3). Note that for the sake of clarity, the vertical axes do not all have the same scale.

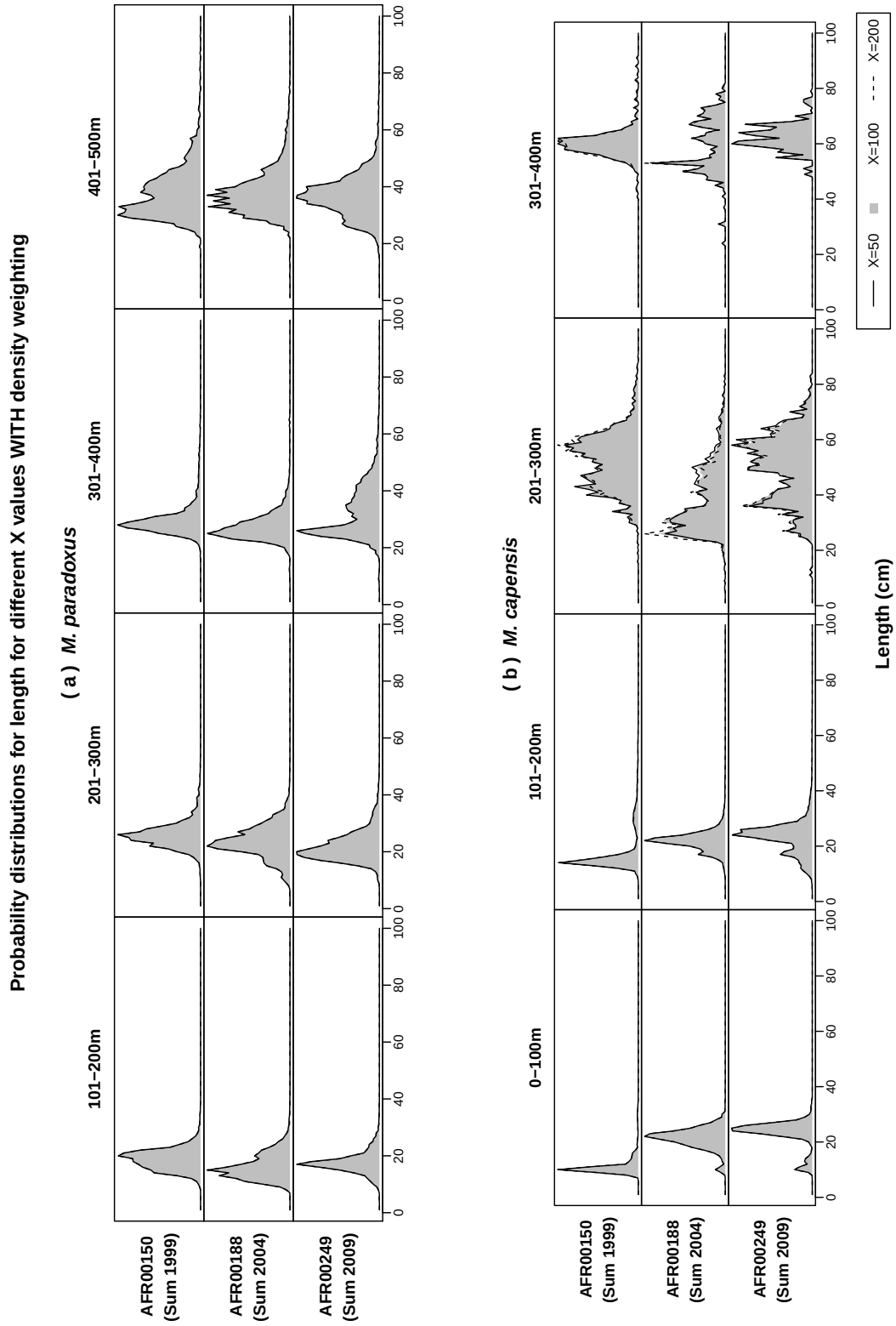

Figure 3.A.2: *M. paradoxus* and *M. capensis* probability distributions for length shown for a selection of three cruises and for three different values of X, the sample size above which sampling variability is assumed to no longer dominate. The results here are for the case when **density weighting is taken into account** (Equation 3.A.5). Note that for the sake of clarity, the vertical axes do not all have the same scale.

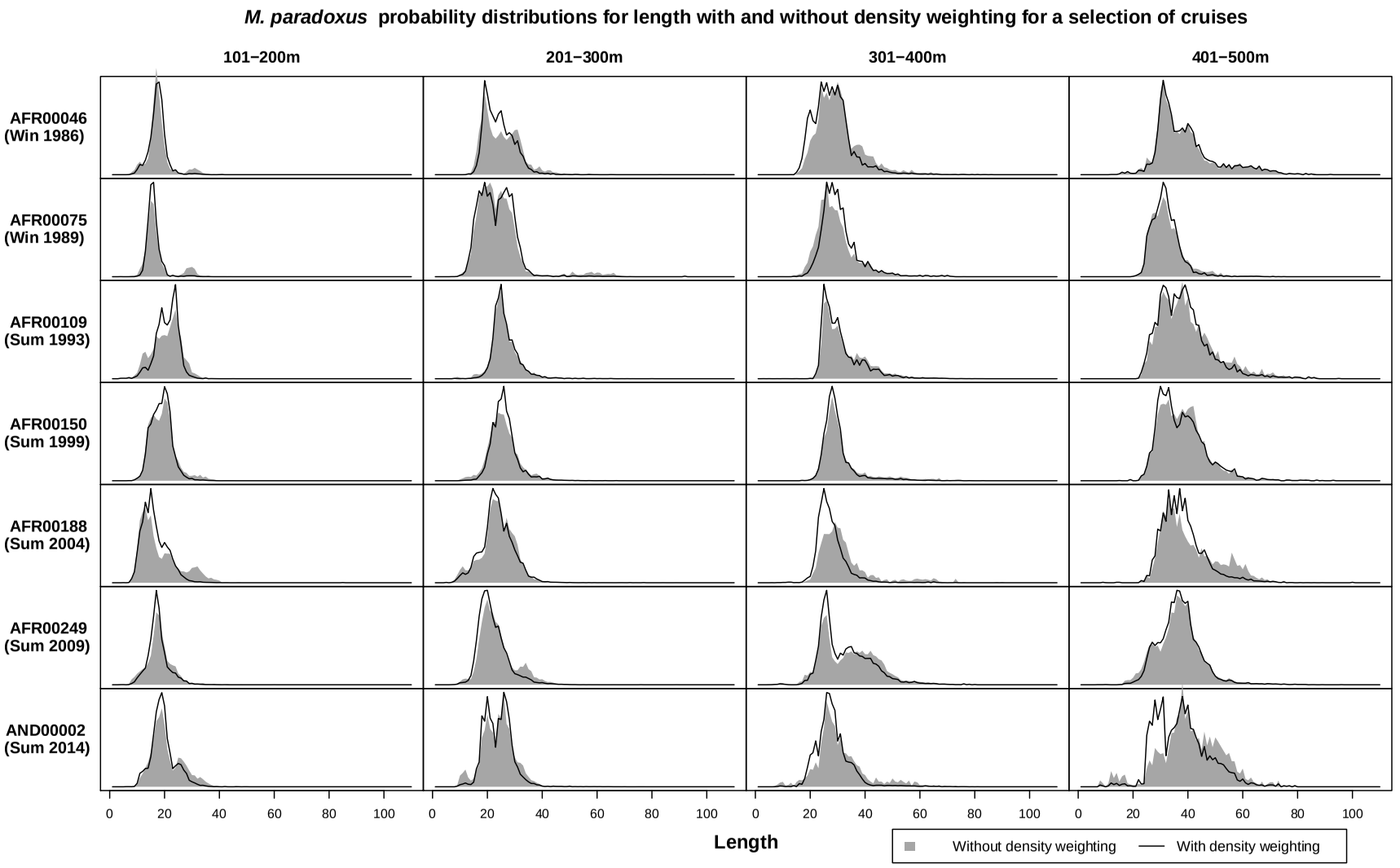

Figure 3.A.3: ***M. paradoxus*** probability distributions for length for each of four depth strata are shown for a selection of cruises for $X = 100$. The grey shaded areas indicate the probability distributions when density weighting is not taken into account (Equation 3.A.3), while the black lines show the probability distributions for when this weighting is taken into account (Equation 3.A.5). Note that for the sake of clarity, the vertical axes do not all have the same scale.

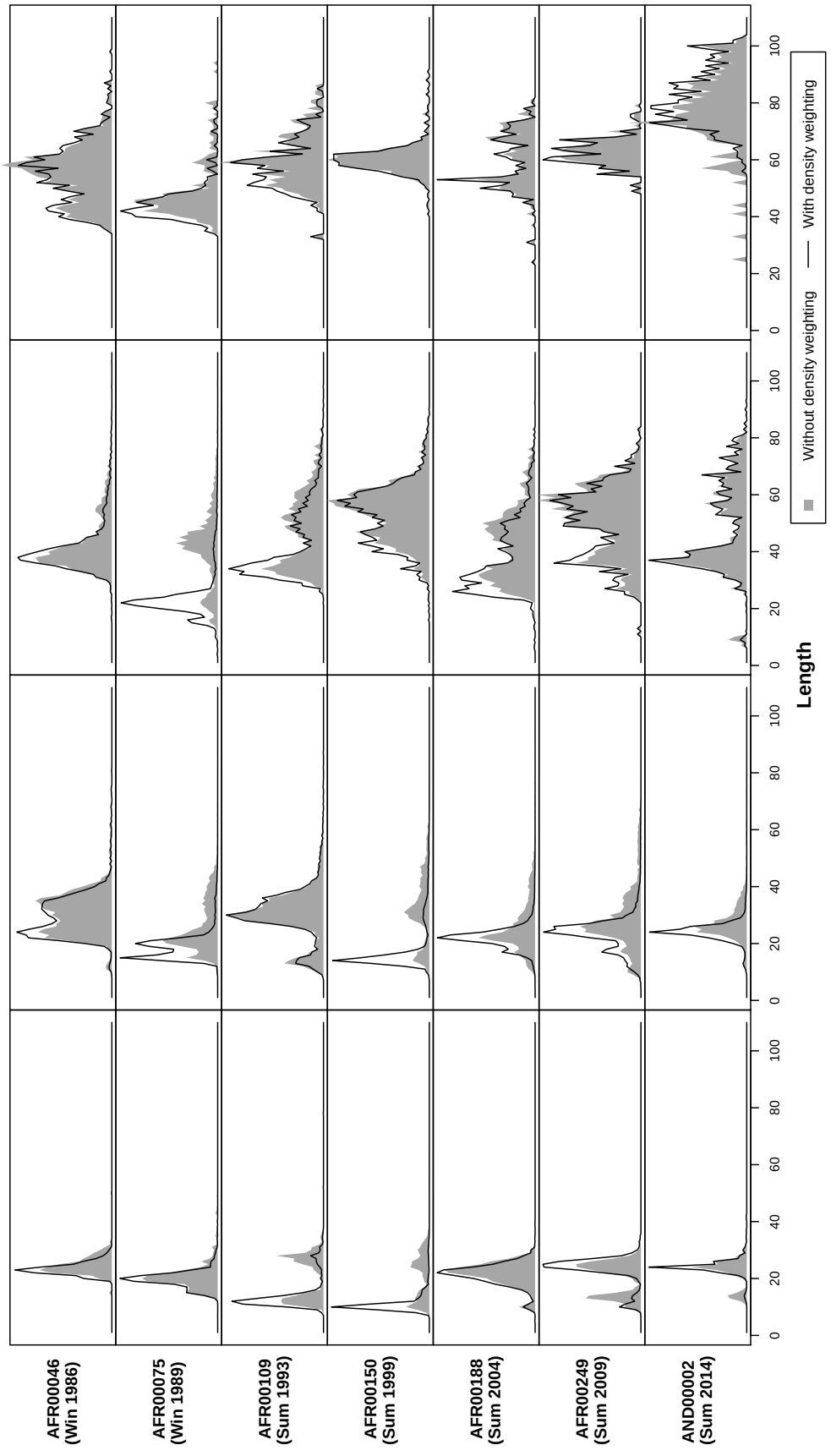

Figure 3.A.4: ***M. capensis*** probability distributions for length for each of four depth strata are shown for a selection of cruises for $X = 100$. The grey shaded areas indicate the probability distributions when density weighting is not taken into account (Equation 3.A.3), while the black lines show the probability distributions for when this weighting is taken into account (Equation 3.A.5). Note that for the sake of clarity, the vertical axes do not all have the same scale.

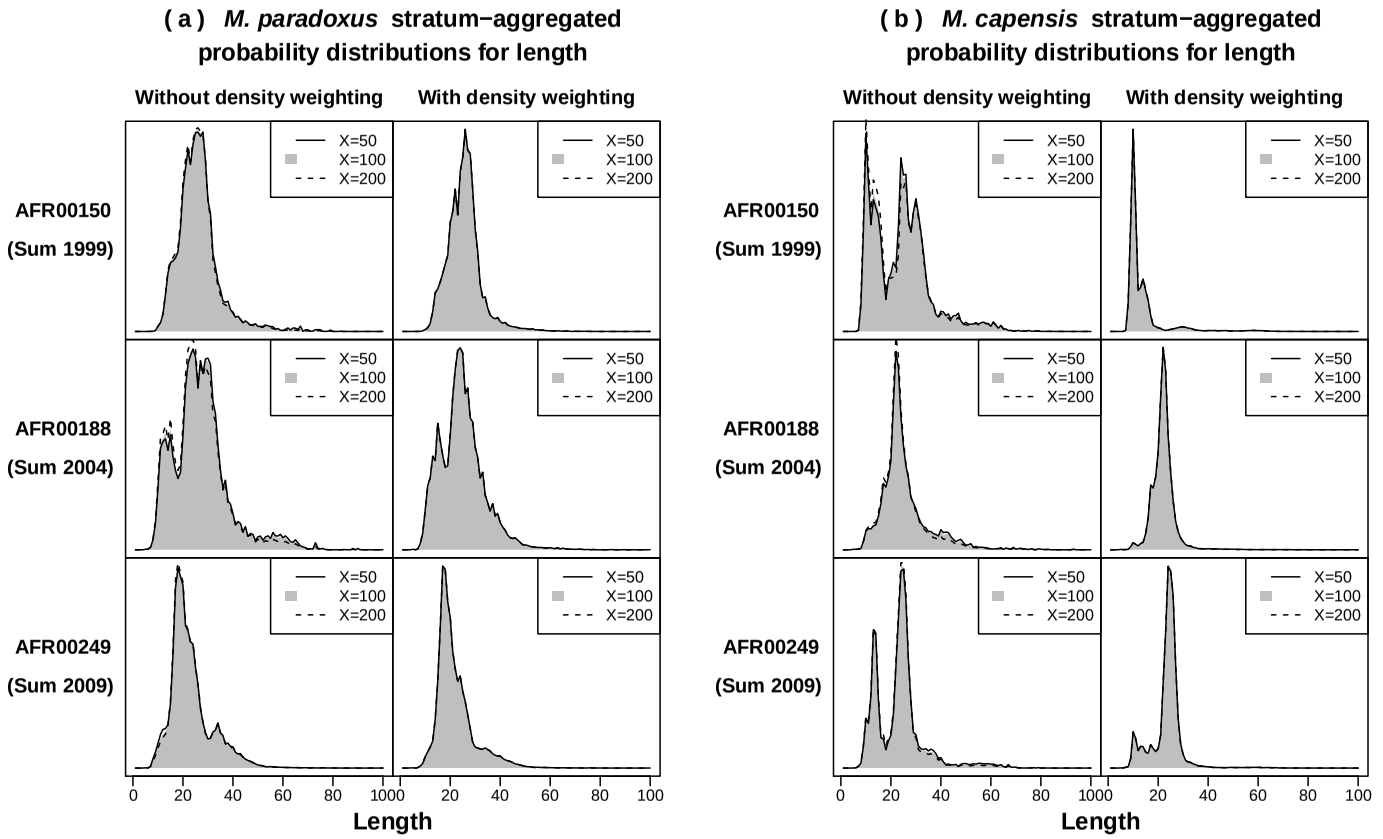

Figure 3.A.5: *M. paradoxus* and *M. capensis* stratum-aggregated probability distributions for length are shown for a selection of three cruises and for **three different values of** X, the sample size above which sampling variability is assumed to no longer dominate. The results are shown for both the case where density weighting is not taken into account and where it is. Note that for the sake of clarity, the vertical axes do not all have the same scale. Note also that the stratum-aggregated proportions were calculated using the methodology of Sen1.

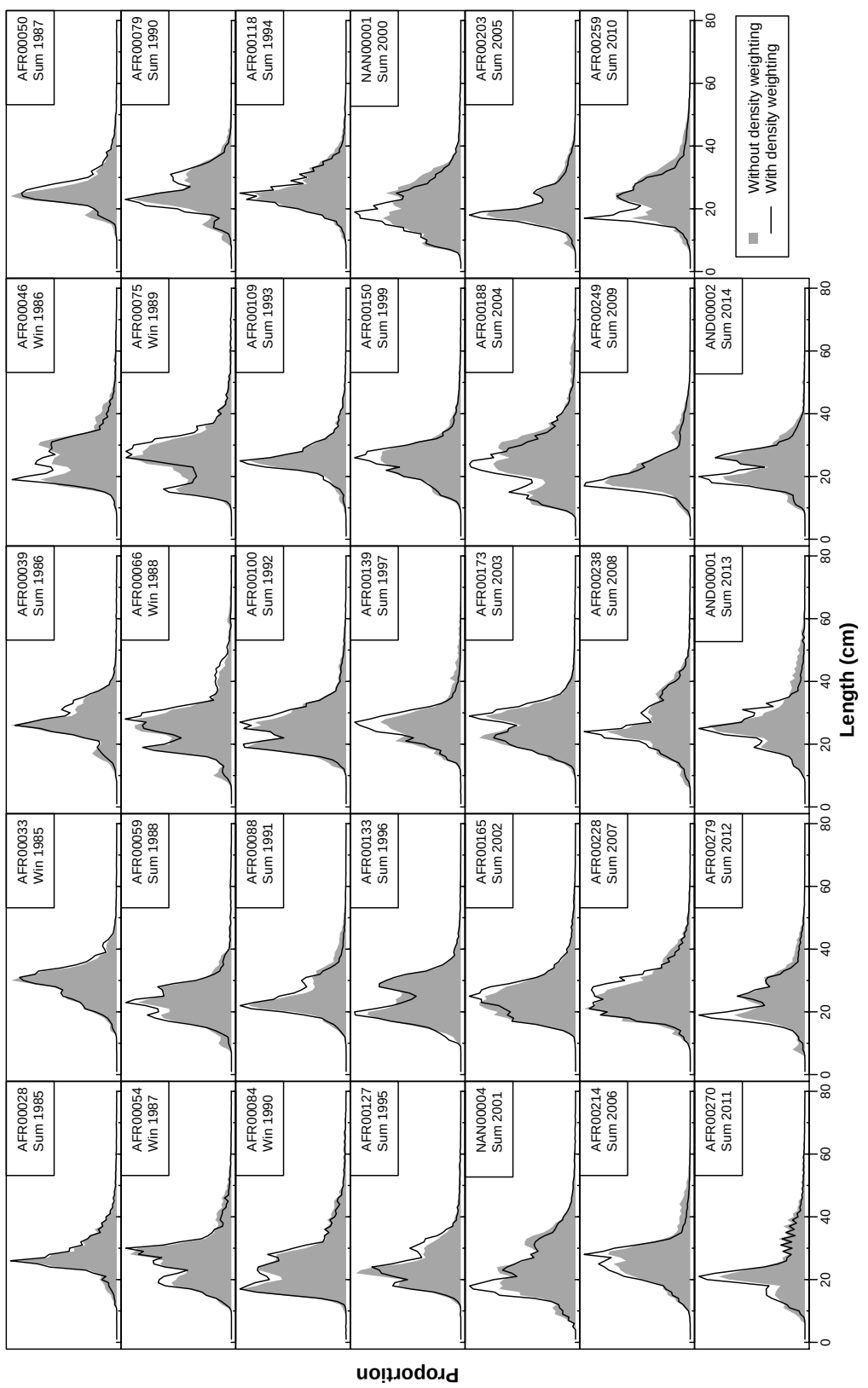

Figure 3.A.6: ***M. paradoxus*** **stratum-aggregated** probability distributions for length are shown for all cruises for $X = 100$. The grey shaded areas indicate the probability distributions when density weighting is not taken into account (Equation 3.A.3), while the black lines show the probability distributions for when this weighting is taken into account (Equation 3.A.5). Note that for the sake of clarity, the vertical axes do not all have the same scale. Note also that the stratum-aggregated proportions were calculated using the methodology of Sen1.

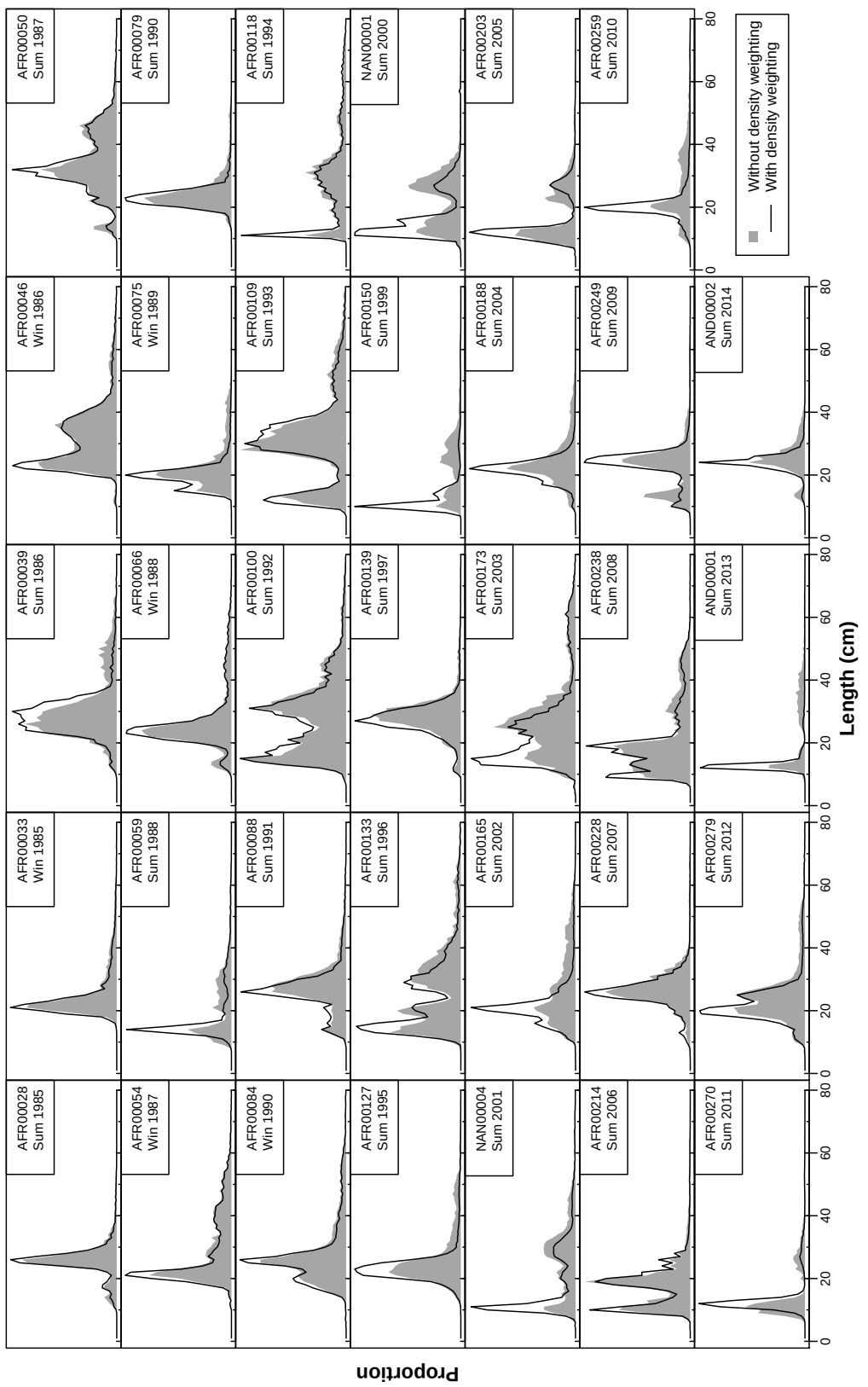

Figure 3.A.7: *M. capensis* stratum-aggregated probability distributions for length are shown for all cruises for $X = 100$. The grey shaded areas indicate the probability distributions when density weighting is not taken into account (Equation 3.A.3), while the black lines show the probability distributions for the this weighting is taken into account (Equation 3.A.5). Note that for the sake of clarity, the vertical axes do not all have the same scale. Note also that the stratum-aggregated proportions were calculated using the methodology of Sen1.

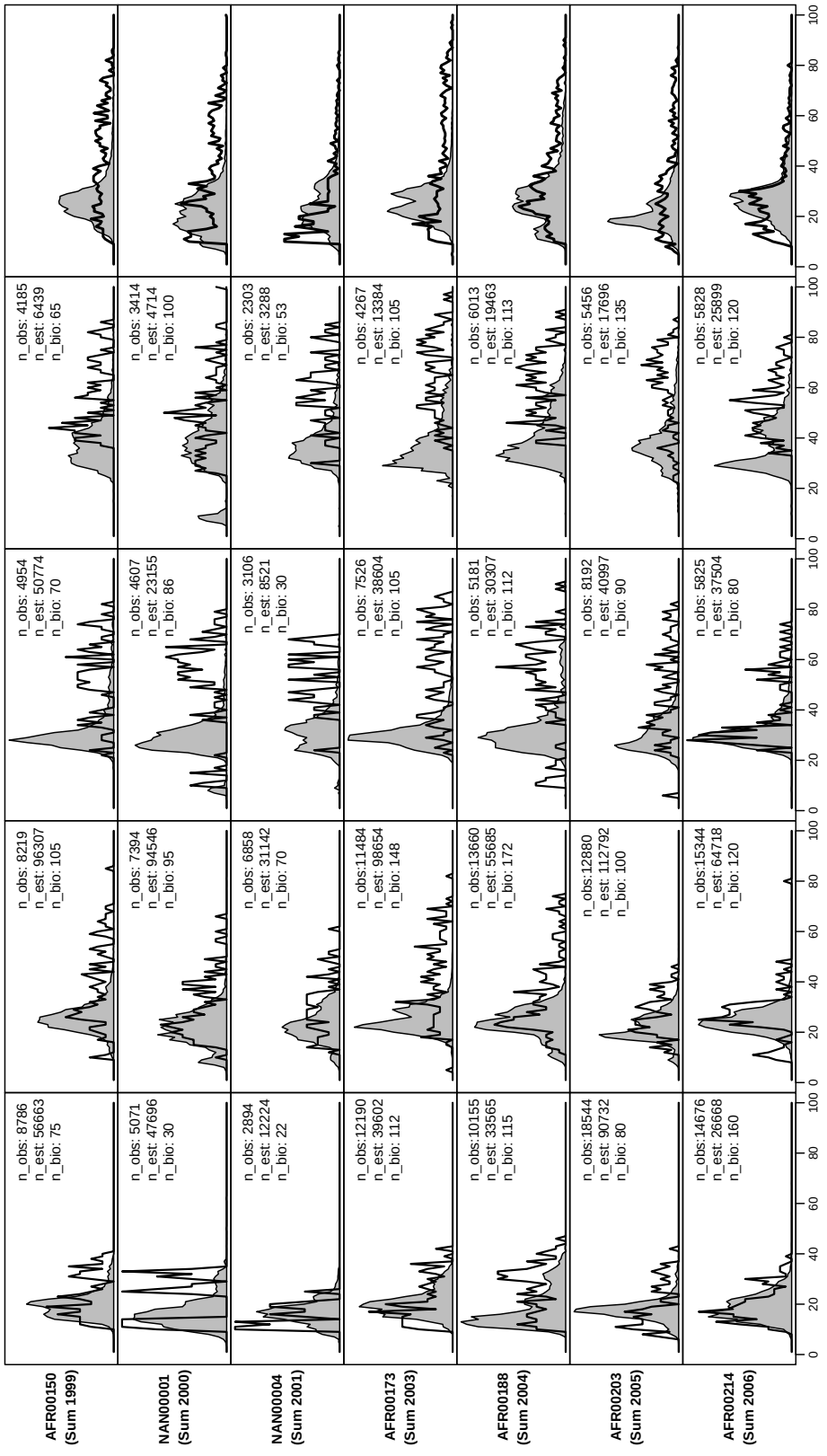

Figure 3.A.8: Comparison of ***M. paradoxus*** survey probability distributions for length without density weighting for $X = 100$ (grey shaded area) with the length-distribution of the sub-sample of the survey catch for which **biological information** was measured (solid black lines). The distributions indicated by the grey shaded area are the same as those for $X = 100$ in Figure 3.A.1(a). Distributions are given by depth stratum for all cruises in Figures 3.A.8 and 3.A.9. The vertical axes here all have the same scale. Note that the stratum-aggregated proportions were calculated using the methodology of Sen1.

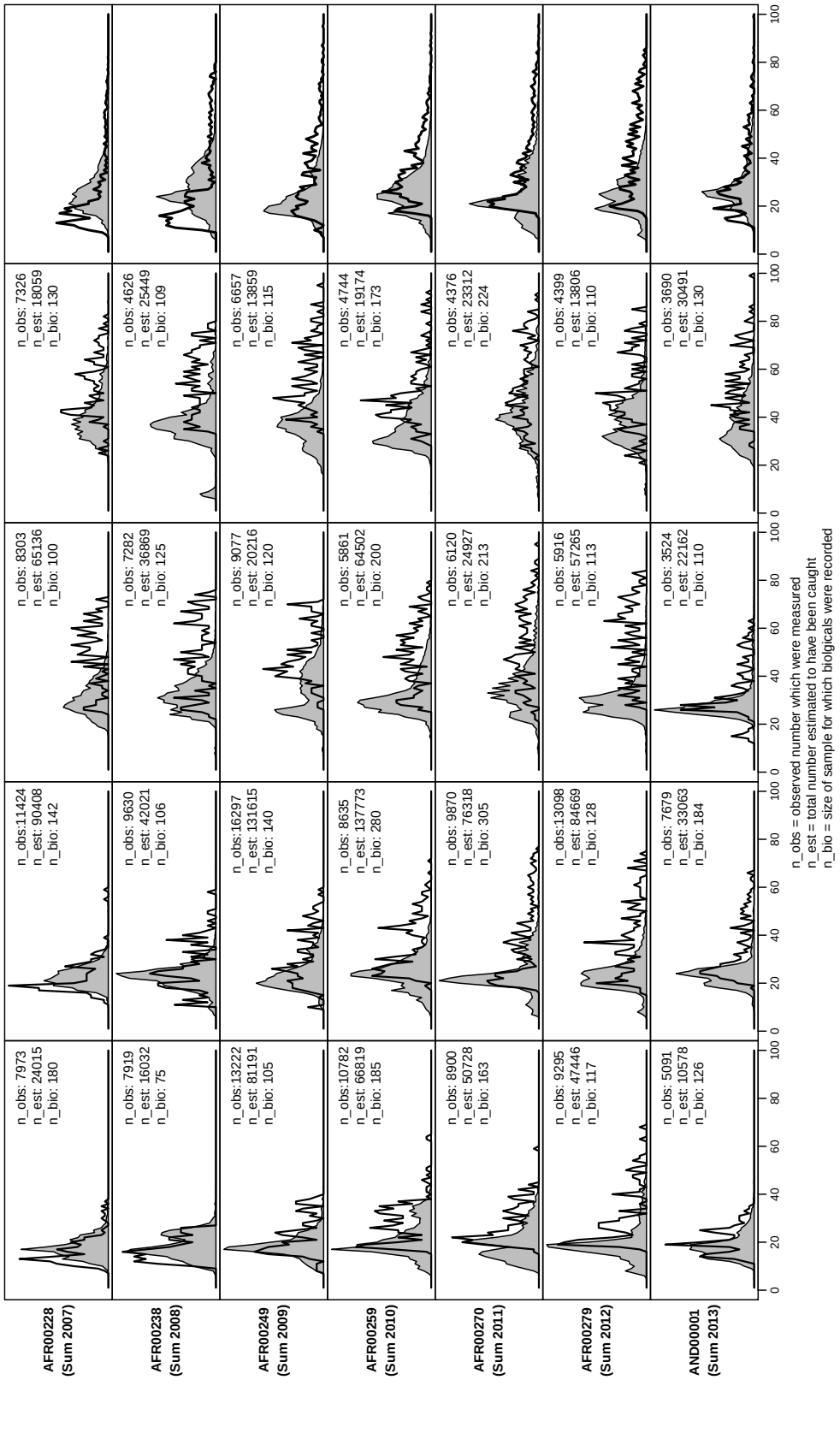

Figure 3.A.9: Continuation of Figure 3.A.8.

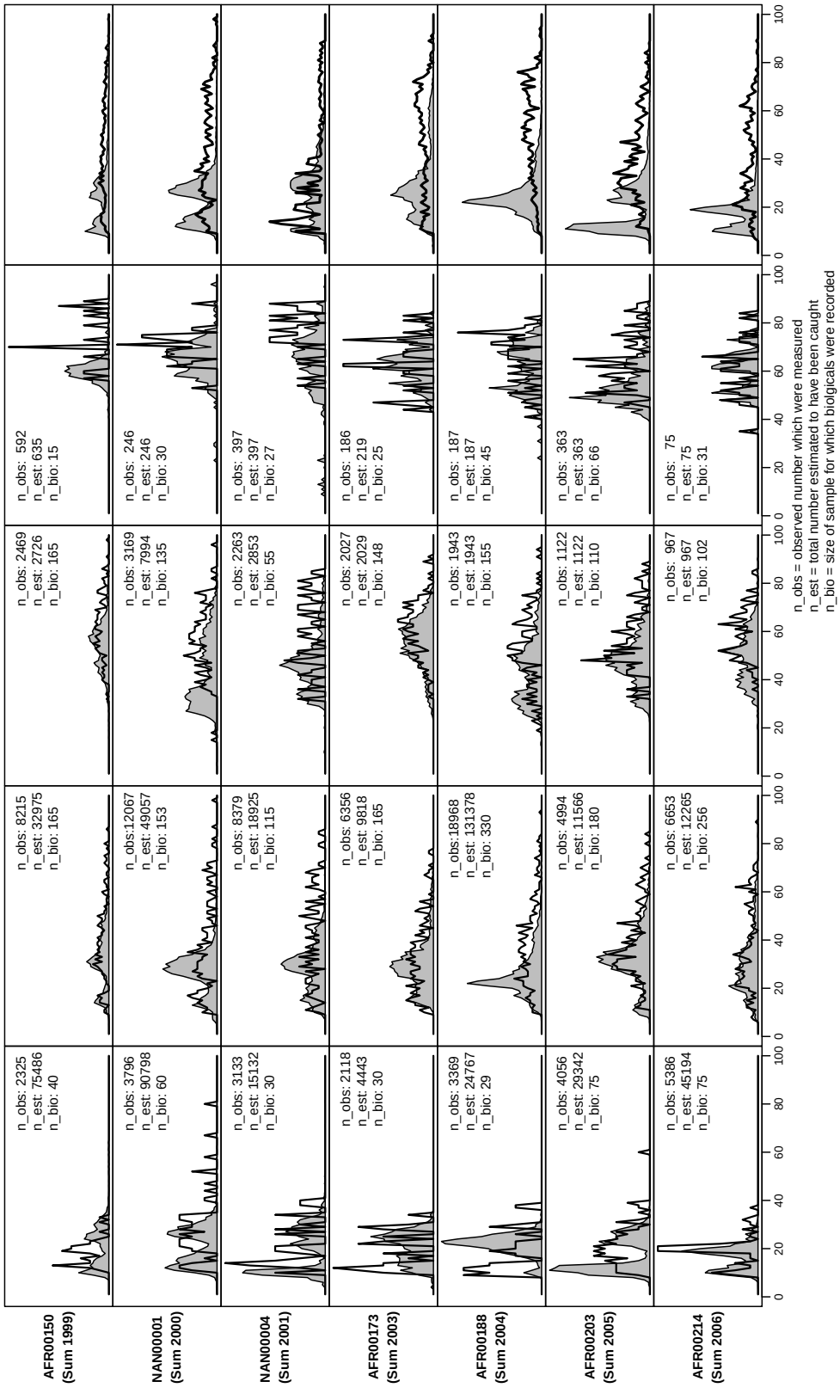

Figure 3.A.10: Comparison of ***M. capensis*** survey probability distributions for length without density weighting for $X = 100$ (grey shaded area) with the length-distribution of the sub-sample of the survey catch for which **biological information** were measured (solid black lines). The distributions indicated by the grey shaded area are the same as those for $X = 100$ in Figure 3.A.1(b). Distributions are given by depth stratum for all cruises in Figures 3.A.10 and 3.A.11. The vertical axes here all have the same scale. Note that the stratum-aggregated proportions were calculated using the methodology of Sen1.

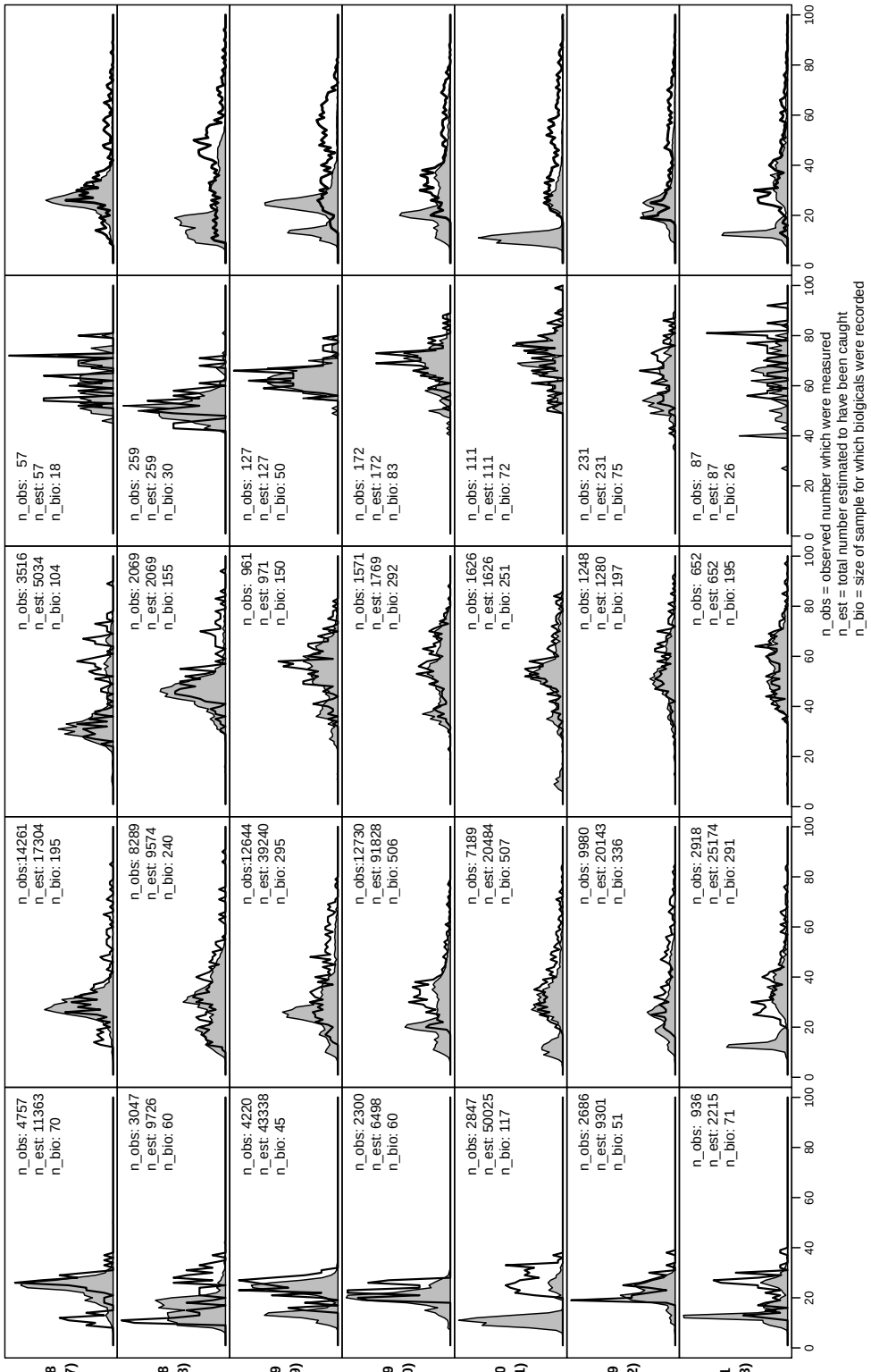

Figure 3.A.11: Continuation of Figure 3.A.10.

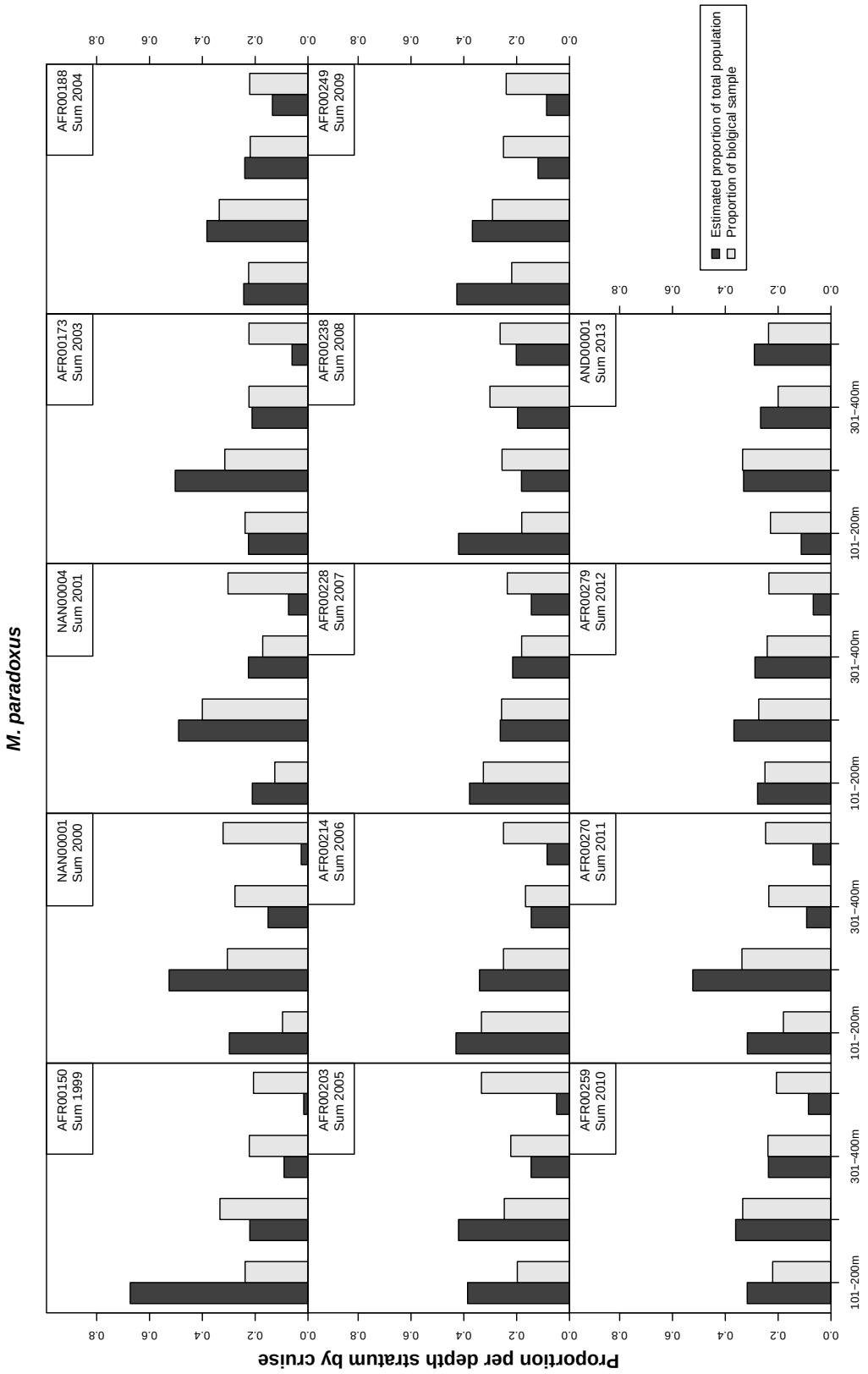

Figure 3.A.12: ***M. paradoxus*** proportion of the total biolgical sample size per depth stratum (light grey bars) plotted in contrast to the proportion of the survey estimate of population size attributed to each stratum (dark grey bars). The population estimate here is the product of the estimated density and the area of each stratum. Results are shown for all cruises for which biological data have been provided for this study. Population estimates are not available for the 501-1000m depth stratum as there was no estimate available for the area of this stratum (which is needed to scale up the survey numbers to an overall population estimate), and also the stratum was not sampled every year within the sampling period.

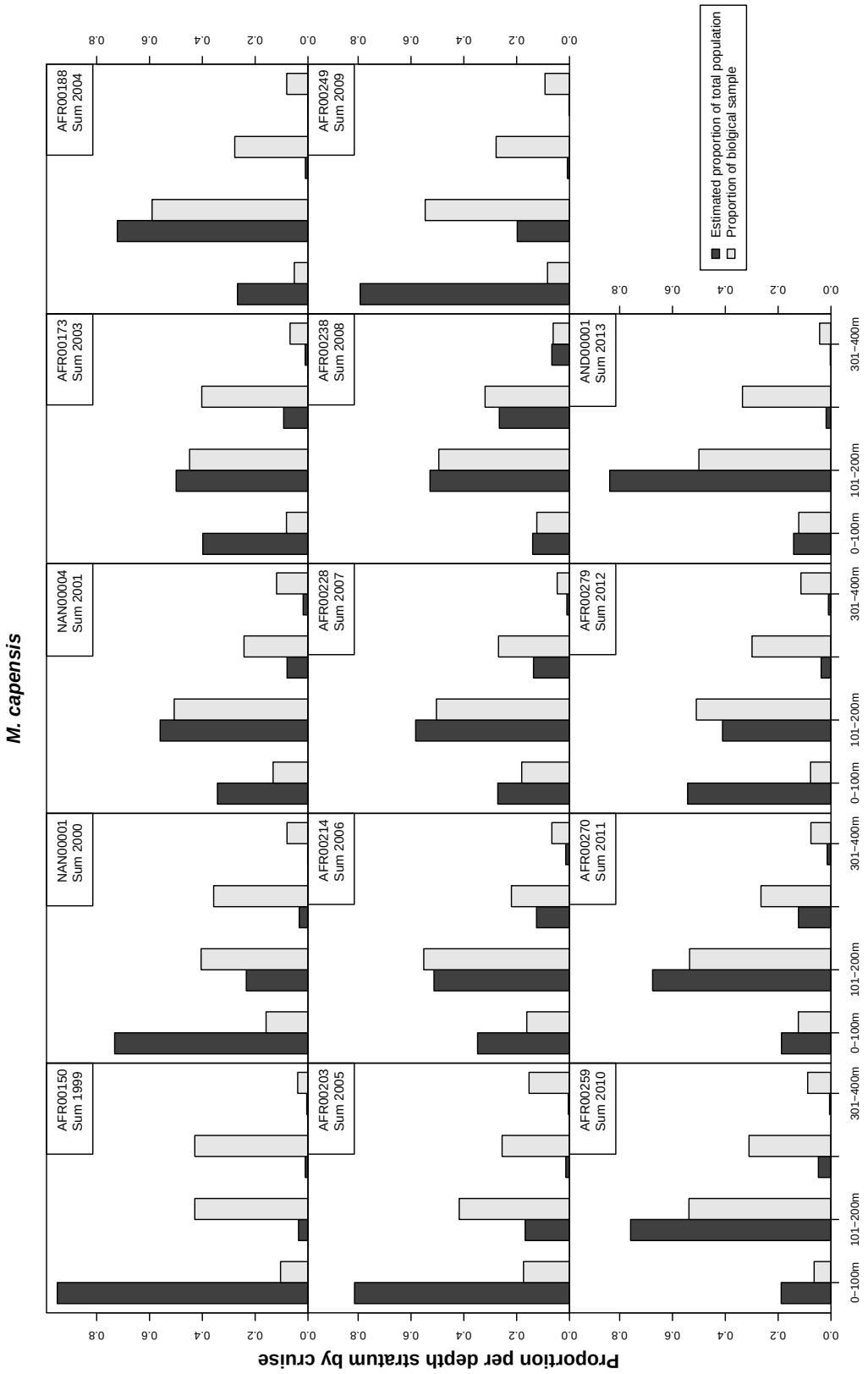

Figure 3.A.13: ***M. capensis*** proportion of total biolgical sample size per depth stratum (light grey bars) plotted in contrast to the proportion of the survey estimate of population size attributed to each stratum (dark grey bars). The population estimate here is the product of the estimated density and the area of each stratum. Results are shown for all cruises for which biological data have been provided for this study.

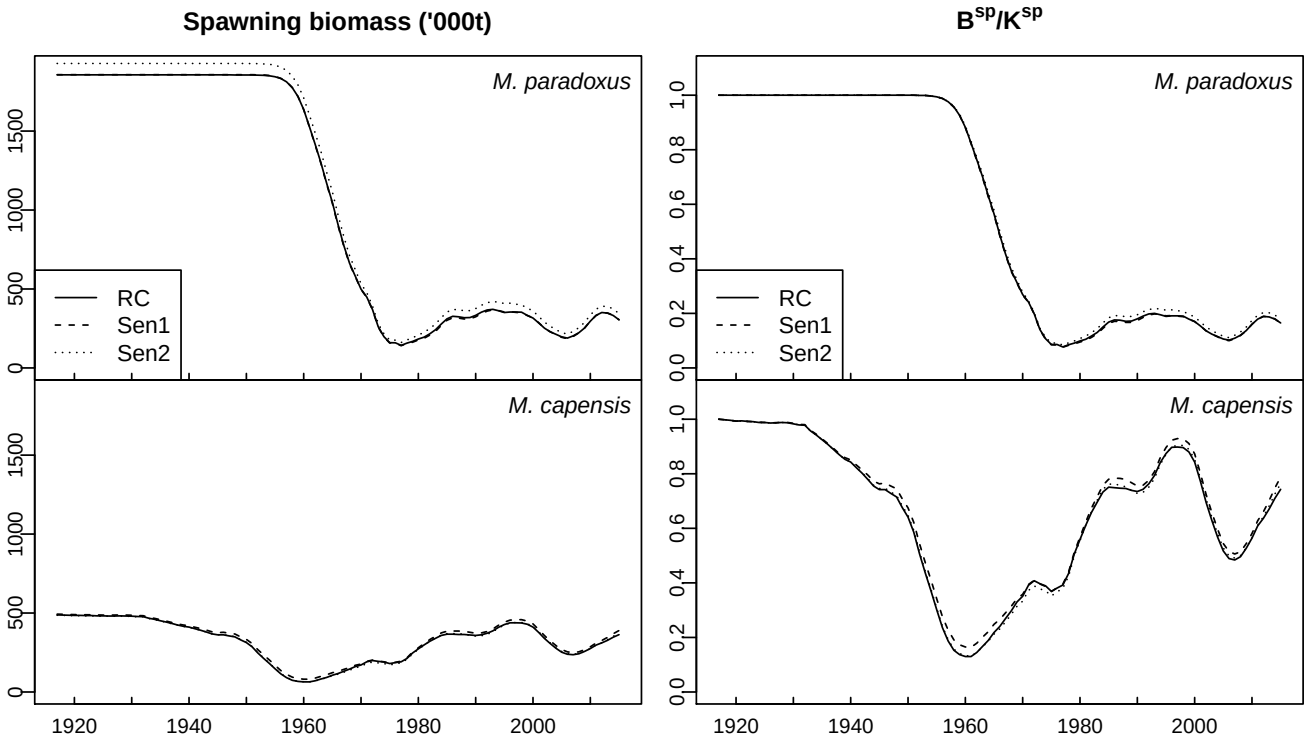

Figure 3.A.14: *M. paradoxus* and *M. capensis* spawning biomasses shown in terms of absolute values and relative to pristine spawning biomass. Results are given for the three cases described in Equation 3.A.8 and immediately thereafter.

RC: No density-weighting; survey estimated population size ($N^{s_p}_{y,d}$ from Equation 3.A.8) is calculated from the survey estimate of spawning biomass. This is the methodology currently in use.

Sen1: No density-weighting; survey estimated population size $N^{s_p}_{y,d}$ is calculated directly from the survey samples.

Sen2: Density-weighting; survey estimated population size $N^{s_p}_{y,d}$ is calculated directly from the survey samples.

Chapter 4

The adjusted Rademeyer and Butterworth (2014b) hake model

Please note that the descriptions and equations in this Chapter are based on those developed by Rademeyer and Butterworth (2014b). They have been included here since they form the foundation of the hake predation model presented in Chapter 5, and in order to highlight the changes that have been made to the original model to structure it more suitably for the extensions to incorporate hake predation.

4.1 Introduction

The equations presented in this Chapter are based on those in Rademeyer and Butterworth (2014b), with a few changes to allow for the readier incorporation of predation mortality (which is described in Chapter 5). The major overall changes are outlined below, while changes that have been made to particular aspects of the model are highlighted in the relevant sections.

1. In the interest of simplicity, given the complicated nature of predator-prey interactions, the predation model is sex-aggregated in its current form. Sex-aggregated versions of the Rademeyer and Butterworth (2014b) equations have thus been presented here, with references to gender removed.

2. The predation model uses a monthly (rather than annual) time step to account for the fact that the predation dynamics are likely to be much faster than the hake dynamics, so that the predation effect would be poorly approximated with a coarser time-step. This monthly time-step has been reflected in the equations presented here, accompanied by further explanations where necessary of the implementation of such a time-step.

3. The predation model implements the Baranov formulation of the catch equation, rather than the Pope approximation as in Rademeyer and Butterworth (2014b). The Baranov formulation has the advantage that catches can never exceed the population size in the model, resulting in greater stability in the estimation process (A. Punt, *pers. comm.*, International Stock Assessment Workshop, December 2013).

4. Rademeyer and Butterworth (2014b) estimate growth curve parameters by fitting directly to age-length keys. The predation model does not fit to age-length keys, and growth parameters are fixed[1] on input based on the Rademeyer and Butterworth (2014b) reference case results.

Some minor editorial changes have been made to the notation used by Rademeyer and Butterworth (2014b), to provide consistency with equations presented in Chapter 5. In summary, the equations presented here describe the basis of the hake model in the form that it has been implemented in the Chapter 5 predation model.

4.2 Population Dynamics

The Rademeyer and Butterworth (2014b) hake model is a fleet-disaggregated, Age-Structured Production Model (ASPM) that assesses the two Cape hake stocks separately (though taking account of the fact that certain data are available on a species-aggregated basis only). Note that in the interest of efficient notation, subscripts in the equations are separated by commas only when this is necessary for the sake of clarity, as was done by Rademeyer and Butterworth (2014b).

4.2.1 Numbers-at-age

The equations for calculating numbers-at-age are first given for the Rademeyer and Butterworth (2014b) model, and then the update that allows for a monthly time-step.

The Rademeyer and Butterworth (2014b) equations

The population numbers-at-age in year $y+1$ are related to the numbers-at-age in year y by assuming that catches are removed from the population at mid-year, following a Pope approximation of the catch equation, and that natural mortality occurs throughout the year:

$$N_{s,a,y+1} = \begin{cases} R_{s,y+1} & \text{for } a = 0 \\ \left(N_{s,a-1,y}e^{-(M_{s,a-1})/2} - \sum_f C_{s,a-1,f,y}\right) e^{-(M_{s,a-1})/2} & \text{for } 0 < a \leq a_m - 1 \\ \left(N_{s,a_m-1,y}e^{-(M_{s,a_m-1})/2} - \sum_f C_{s,a_m-1,f,y}\right) e^{-(M_{s,a_m-1})/2} + & \\ \qquad \left(N_{s,a_m,y}e^{-(M_{s,a_m})/2} - \sum_f C_{s,a_m,f,y}\right) e^{-(M_{s,a_m})/2} & \text{for } a = a_m \end{cases} \tag{4.1}$$

where

N_{say}	is the number of fish of species s and age a at the start of year y,
R_{sy}	is the recruitment of fish (number of zero year old fish) of species s at the start of year y,
a_m	is the maximum age considered in the model (taken to be a plus-group),
M_{sa}	is the natural mortality rate on fish of species s and age a, and
C_{safy}	is the number of hake of species s and age a caught in year y by the fisheries fleet f.

[1] Not incorporating feedback of predation into growth rates is a standard approach to estimating mortality in multi-species models (S. Gaichas, *pers. comm.*).

Adjustments for the monthly time-step

Let the subscript m denote month. The use of a monthly time step, as well as the fact that recruitment is assumed to occur each month (see Section 4.2.2), means that the model needs to take the growth of individual fish into account throughout the year. A fish aged one month for example will not be the same size as a fish aged 11 months, even though both would be classed as 'zero year old' hake. As such, the model keeps track of the number of hake in each age-class by *month* and uses these for the basic calculations. Let $\widetilde{N}_{s,\tilde{a},y,m}$ be the number of hake aged $\tilde{a}$ *months*. Then, assuming a Baranov formulation for the catch equation, rather than Pope's approximation, the number of hake aged $\tilde{a}+1$ months in the following month is given by:

$$\widetilde{N}_{s,\tilde{a}+1,y,m+1} = \widetilde{N}_{s,\tilde{a},y,m} e^{-Z_{saym}} \tag{4.2}$$

where Z_{saym} is the total mortality for hake of species s and age a years in month m of year y, and is given by:

$$Z_{saym} = M_s^{basal}/12 + P_{saym} + \sum_f S_{saf} F_{sfym} \tag{4.3}$$

where M_s^{basal} is the basal natural mortality rate, P_{saym} is the mortality due to hake-on-hake predation, S_{saf} is the selectivity of fishing fleet f on hake of species s and age a, and F_{sfym} is the fully selected instantaneous fishing mortality of fleet f on hake of species s in month m of year y. Full details of the first two sources of mortality are provided in Chapter 5, and details of the fishing mortality in Section 4.2.7.

Note that for the month of January (i.e. $m=1$), $\widetilde{N}_{s,a+1,y,1} = \widetilde{N}_{s,a,y-1,12} e^{-Z_{s,a,y-1,12}}$.

The number of hake aged a years is then given by:

$$N_{saym} = \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s,\tilde{a},y,m} \tag{4.4}$$

4.2.2 Recruitment

Rademeyer and Butterworth (2014b) assume the number of new recruits (i.e. zero-year old fish) at the start of each year is a function of the female spawning biomass. Since the predation model presented in this thesis is sex-aggregated, total spawning biomass has been used instead. The relationship between recruitment and spawning biomass is characterised by a Beverton-Holt (Beverton and Holt 1957) stock-recruitment relationship:

$$R_{sy} = \frac{\alpha_s B_{sy}^{sp}}{\beta_s + B_{sy}^{sp}} \, e^{(\zeta_{sy} - \sigma_R^2/2)} \tag{4.5}$$

where

R_{sy}	is the recruitment in year y,
B_{sy}^{sp}	is the spawning biomass of species s in year y,
ζ_{sy}	reflects fluctuation about the expected recruitment for species s in year y,
σ_R	is the standard deviation of the log of the recruitment residuals, which is fixed on input (see Section 4.3.5), and
α_s, β_s	are parameters.

Let h be the steepness of the stock-recruitment curve, corresponding to the fraction of the recruitment under pristine conditions, R_{s0}, that results when spawning biomass drops to 20% of its pristine level. The parameters

α_s and β_s can then be determined by:

$$\alpha = \frac{4hR_{sy_0}}{5h-1} \tag{4.6}$$

and

$$\beta = \frac{K_s^{sp}(1-h)}{5h-1} \tag{4.7}$$

where

K_s^{sp}	is the pre-exploitation equilibrium spawning biomass for species s,
R_{sy_0}	is the recruitment for species s at equilibrium, and
h	is the steepness of the stock-recruitment curve.

Adjustments for the monthly time-step

In light of the monthly time-step of the predation model, recruitment is assumed to take place continually throughout the year[2], at the start of each month, i.e. a twelfth of the recruitment that would normally be determined by the Beverton-Holt relationship in a year is allocated to each month, but calculated from the spawning biomass in that month. Equation 4.5 becomes:

$$R_{sym} = \left(\frac{1}{12}\right) \frac{\alpha_s B_{sym}^{sp}}{\beta_s + B_{sym}^{sp}} \, e^{(\zeta_{sy} - \sigma_R^2/2)} \tag{4.8}$$

Here, R_{sym} and B_{sy}^{sp} are respectively the recruitment and spawning biomass in month m of year y (see Section 4.2.3 for the definition of the monthly spawning biomass). Further, Equation 4.6 is adjusted to:

$$\alpha = \frac{4h(12R_{sy_0,m_0})}{5h-1} \tag{4.9}$$

where R_{sy_0,m_0} is the recruitment of age zero (*in months*) hake in the first month considered in the model (see Chapter 5 for details of the equilibrium set-up).

Rademeyer and Butterworth (2014b) implement both the Beverton Holt and a modified Ricker stock-recruitment relationship, and in fact assume the modified Ricker relationship for their base case assessment. The predation model implements the Beverton-Holt stock-recruitment relationship in its base case model[3] (and fixes h at 0.9 to aid stability, given that h is poorly estimated, but likely high, in terms of the Rademeyer and Butterworth 2014b model), and the Ricker formulation is included only as a sensitivity test, along with a run that estimates the h for the Beverton-Holt formulation. The modified Ricker was not implemented for the base case because of difficulties that arose early in the model development process when trying to estimate the γ parameter, and as such the simpler Beverton-Holt relationship was preferred (although the modified Ricker relationship may well become the base case assumption in future developments of the model.)

[2]Although studies have shown hake to exhibit peak spawning periods, spawning does appear to occur throughout the year, so this assumption is unlikely to introduce any major bias. However, since combining seasonal recruitment with seasonal growth may well lead to more variation than assuming a constant rate of recruitment, sensitivity to this assumption of constant recruitment has been noted for future work (see Chapter 7).

[3]The modified Ricker is implemented in the Rademeyer and Butterworth (2014b) base case model as there is evidence of decreasing recruitment at larger spawning biomass.

4.2.3 Spawning Biomass

The spawning biomass is calculated on a monthly basis and takes the weight of hake into account based on their age in months:

$$B^{sp}_{sym} = \sum_{a=1}^{a_m} f_{sa} \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}ym} w_{s\tilde{a}} \tag{4.10}$$

where

f_{sa}	is the proportion of fish of species s and age a that are mature (see Section 4.2.5) ,
$\widetilde{N}_{s\tilde{a}ym}$	is the number of hake of species s and age $\tilde{a}$ months in month m of year y, and
$w_{s\tilde{a}}$	is the mass of a hake of species s and age $\tilde{a}$ months.

4.2.4 Natural mortality

The predation model assumes an age-independent basal natural mortality, to which the effects of predation are added (see Chapter 5). For the purpose of comparison of the results of the predation model to those from the Rademeyer and Butterworth (2014b) model, the specifications of the natural mortality for the latter have been included here. There, natural mortality (M_{sa}) is assumed to be related to age by the following function:

$$M_{sa} = \begin{cases} M_{s,2} & \text{for } a \leq 1 \\ \alpha^M_s + \frac{\beta^M_s}{a+1} & \text{for } 2 \leq a \leq 5 \\ M_{s,5} & \text{for } a > 5 \end{cases} \tag{4.11}$$

Since hake of ages two and younger seldom occur in catch and survey data, $M_{s,0}$ and $M_{s,1}$ cannot be independently estimated and are set equal to $M_{s,2}$. The Rademeyer and Butterworth (2014b) reference case model fixes $M_{s,2}$ at 0.75 and $M_{s,5}$ at 0.375, effectively fixing α^M_s and β^M_s on input.

4.2.5 Length- and age-at-maturity

The proportion of fish of species s and length l that are mature is assumed to follow a logistic curve with the parameter values given in Table 4.1:

$$f_{sl} = \left(1 + e^{\frac{l - l_{s,50}}{\Delta_s}}\right)^{-1} \tag{4.12}$$

Maturity-at-length is then converted to maturity-at-age as follows:

$$f_{sa} = \sum_l f_{sl} A_{sal} \tag{4.13}$$

where A_{sal} is the proportion of fish of species s and age a that fall into the length group l (i.e. $\sum_l A_{sal} = 1$ for all ages a). This matrix is calculated assuming that length-at-age is log-normally distributed about a central value given by the von Bertalanffy equation:

$$lnl_{sa} \sim N\left[ln\left(l_{s,\infty}\left(1 - e^{-\kappa_s(a - t_{s,0})}\right)\right); \left(\frac{\sigma^A_{sa}}{l_{s,\infty}\left(1 - e^{-\kappa_s(a - t_{s,0})}\right)}\right)^2\right] \tag{4.14}$$

where σ^A_{sa} is the standard deviation of the length-at-age for a fish of species s and age a, which is fixed for age zero, and a linear relationship is fit for ages one and above:

$$\sigma^A_{sa} = \begin{cases} \sigma^A_{s,0} & \text{for } a = 0 \\ \beta^A_s a + \alpha^A_s & \text{for } 1 \leq a \leq a_m \end{cases} \tag{4.15}$$

The Rademeyer and Butterworth (2014b) model estimates $\sigma^A_{s,0}$, α^A_s and β^A_s in the model fitting procedure, with $\beta^A_s > 0$ so that σ^A_{sa} increases with age. Since the predation model does not fit to age-length keys, it would have difficulty estimating these parameters, and the estimates of the Rademeyer and Butterworth (2014b) have been used instead. These estimates are listed in Table 4.2.

4.2.6 Weight-at-length and weight-at-age

The weight of a fish of species s and length l is calculated as follows:

$$w_{sl} = \alpha(l)^\beta \tag{4.16}$$

where the values of α and β are given in Table 4.3. Weight-at-length is converted to weight-at-age as for maturity-at-age:

$$w_{sa} = \sum_l w_{sl} A_{sal} \tag{4.17}$$

4.2.7 Total catch and catches-at-age

Commercial catches are assumed to be taken continually throughout the year, after recruitment and predation have been taken into account each month. In accordance with the Baranov catch formulation, the number of fish of species s and age a caught in month m of year y by fleet f is given by:

$$C_{safym} = S_{safy} F_{sfy} N_{saym} \frac{(1 - e^{Z_{saym}})}{Z_{saym}} \tag{4.18}$$

where

F_{sfy} is the fishing mortality of a fully selected age class, for fleet f in year y, and

S_{safy} is the fishing selectivity by fleet f on fish of species s and age a in the year y, which is calculated from the selectivity-at-length S_{slfy} (see Section 4.2.10):

$$S_{safy} = \sum_l S_{slfy} A_{sal} \tag{4.19}$$

The total fleet disaggregated catch, by mass, for species s in month m of year y, is calculated taking the mass of hake by their age in months into account:

$$C_{sfym} = \sum_{a=0}^{a_m} S_{safy} F_{sfy} \frac{(1 - e^{Z_{saym}})}{Z_{saym}} \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}ym} w_{s\tilde{a}} \tag{4.20}$$

4.2.7.1 Differences to the Rademeyer and Butterworth (2014b) model

The formulation above for the catches differs somewhat from the original Rademeyer and Butterworth (2014b) approach, in the following ways.

- Rademeyer and Butterworth (2014b) assume that the catches are taken at mid-year, and as such utilise the mid-year population numbers and biomasses. Since the predation model tracks the population and deducts catches on a monthly basis, the monthly estimates of population size are used directly.
- The Rademeyer and Butterworth (2014b) model works with a selectivity-weighted mass-at-age function when calculating catches in Equation 4.20. In other words, catches-at-age for fleet f are calculated from a biomass "available" to that fleet, given its fishing selectivity. It was found that implementing this selectivity-weighted mass-at-age greatly increased the computation demands of the predation model, so that this aspect (which is unlikely to have a substantial effect) has not been included.
- The use of the Pope approximation for catches as in Rademeyer and Butterworth (2014b) allows the fishing mortality rates F_{safym} to be calculated analytically from the recorded catches. For the Baranov approach, these fishing mortality rates normally need to be estimated in the model, which dramatically increases the number of estimable parameters. Following a recommendation made at the 2013 International Stock Assessment Workshop (Smith *et al.* 2013), the predation model implements a hybrid method (see Appendix 4.A) that calculates the fishing mortality through an iterative process, allowing the Baranov catch formulation to be implemented without increasing the number of estimable parameters.

In the Pope approach, catches are always set to their observed values, and the population numbers are constrained to remain positive. In the Baranov approach implemented through the hybrid method, the catches are constrained so that the population remains positive, and a penalty is added to the negative log-likelihood for the difference between the observed and model-predicted catches (see Section 4.3.6 for details of this penalty). The latter approach is advantageous in that (a) there is generally at least some extent of uncertainty regarding the observed catches, and this approach allows the model some flexibility in taking them into account, and (b) the approach exhibits much greater stability in the estimation process.

4.2.8 Exploitable and survey biomass

The model estimate of the exploitable biomass, or the component of the biomass available to each commercial fishing fleet, is used to compare the model outputs to the CPUE trend data. The exploitable biomass is calculated at mid-year, i.e. at the beginning of July:

$$B^{\text{exp}}_{sfy} = \sum_{a=0}^{a_m} S_{safy} \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}y,m=7} w_{s\tilde{a}} \tag{4.21}$$

The model-estimated biomass available to survey i, used to compare to survey abundance estimates (in mass), is given by:

$$B^{\text{surv},i}_{sy} = \sum_{a=0}^{a_m} S^{\text{surv},i}_{say} \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}y,m_i} w_{s\tilde{a}} \tag{4.22}$$

$S_{say}^{\text{surv},i}$ is the fishing selectivity for survey i (see following section). The month index m_i is taken to be 1 (January) for the summer surveys, 4 (April) for the autumn surveys, 7 (July) for the winter surveys and 10 (October) for the spring surveys.

4.2.9 Survey fishing selectivity-at-length

The survey selectivities are estimated directly for seven pre-specified lengths for *M. paradoxus* and *M. capensis*. These lengths (given in Table 4.4) are survey specific at constant intervals between the minus (l_{minus}) and plus (l_{plus}) length groups considered for the survey in question. Between these lengths, selectivity is assumed to change linearly. The slope between the selectivity estimated for lengths $l_{minus}+1$ to l_{minus} is assumed to continue exponentially to lower lengths, and similarly the slope between the selectivity at lengths $l_{plus}-1$ to l_{plus} to continue for greater lengths. More explicitly, the slopes are defined as follows:

$$s_{l\min} = ln(S_{l_{minus}+1}/S_{l_{minus}}) \tag{4.23}$$

$$s_{l\max} = ln(S_{l_{plus}}/S_{l_{plus}-1}) \tag{4.24}$$

For lengths less than l_{minus}, $S_{slfy} = S_{s,l+1,fy}e^{-s_{l\min}}$ and for lengths greater than l_{plus}, $S_{slfy} = S_{s,l-1,fy}e^{-s_{l\max}}$. Note that if either $s_{l\min}$ or $s_{l\max}$ are negative, they are set to zero.

In order to prevent severe fluctuations in the selectivity curve, a smoothing penalty is added to the total negative log-likelihod, which penalises deviations from a linear dependence:

$$pen^{surv} = \sum_i \sum_{L=L_1+1}^{L_7-1} 3\left(S_{L-1}^i - sS_L^i + S_{L+1}^i\right)^2 \tag{4.25}$$

Here i is a combination of survey and species, and L_1, $L_2, \ldots, L_7$ are the seven lengths at which selectivity is estimated. Rademeyer and Butterworth (2014b) made the choice of a weighting of 3 empirically so that this term has sufficient but not excessive influence.

Note that separate selectivities are estimated for the new gear that was phased in from 2003, but that are estimated for five lengths only since the same selectivity as the old gear is assumed for older fish.

4.2.10 Commercial fishing selectivity-at-length

The fishing selectivity-at-length for each species and fleet, S_{slfy}, is estimated by means of a double normal curve[4] given by:

$$S_{slfy} = \begin{cases} exp\left(-\frac{(l-l_{y,max})^2}{2\sigma_{y,left}^2}\right) & \text{for } l \le l_{max} \\ exp\left(-\frac{(l-l_{y,max})^2}{2\sigma_{y,right}^2}\right) & \text{for } l > l_{max} \end{cases} \tag{4.26}$$

where $\sigma_{y,left}$, $\sigma_{y,right}$ and $l_{y,max}$ are estimable parameters.

Some further assumptions have been made regarding periods of fixed and changing selectivity for the offshore trawl fleet, to account for a likely change in fishing selectivity as the illegal use of net liners to enhance catch

[4]The use of a double normal curve is necessary as there is a sharp drop in numbers of larger hake evident in the catch-at-length data, probably resulting from a combination of natural mortality, fishing mortality and fishing gear selectivity.

rates was phased out during the 1980s. Rademeyer and Butterworth (2014b) further assume different periods of selectivity for the longline fleet and estimate a separate selectivity for each species and coast, but the predation model estimates just a single selectivity for each coast, which was found to be sufficient. Details of the fishing selectivities and the number of estimable parameters estimated are shown in Table 4.5.

4.2.11 Minus- and plus-groups

Data corresponding to the smallest and largest length classes can exhibit substantial variance, because a relatively small number of fish for these classes is generally caught by the fisheries and surveys. To counter this effect, the assessment is conducted with minus- and plus-groups obtained by summing the data over the lengths below and above l_{minus} and l_{plus} respectively. The minus- and plus-groups used are given in Table 4.6 as they have been applied for the survey and commercial data. Furthermore, the proportions-at-length data (both commercial and survey) are summed into 2cm length classes for the model fitting.

4.3 The likelihood function

The Rademeyer and Butterworth (2014b) model is fit to CPUE and survey biomass indices, commercial and survey length frequencies, survey age-length keys, as well as to the stock-recruitment curve. Contributions to the negative log-likelihood ($-lnL$) are described below for each of these, except for age-length keys since the predation model do not fit to these. Note that strictly speaking this is a penalised log-likelihood, which is maximised in the fitting process, as some contributions are added that would constitute log priors in a Bayesian estimation process (Rademeyer and Butterworth 2014b).

4.3.1 CPUE relative biomass data

Two types of commercial relative biomass indices are available for hake: a species-aggregated historical CPUE series for the West and South coasts, and more recent species-disaggregated GLM-standardised series for the West and South coasts (these series are described in Chapter 3). The likelihood contribution for any given series is calculated by assuming that the observed biomass index is log-normally distributed about its expected value:

$$I_y^i = \hat{I}_y^i e^{\epsilon_y^i} \tag{4.27}$$

where

I_y^i	is the biomass estimate index for year y and series i,
$\hat{I}_y^i = \hat{q}^i \hat{B}_{sfy}^{\exp}$	is the corresponding model estimate, where $\hat{B}_{sfy}^{\exp}$ is the model estimate of exploitable biomass (Equation 4.21),
$\hat{q}^i$	is an estimated constant of proportionality (the catchability coefficient) for biomass series i (see Equation 4.29), and
ϵ_y^i	is taken from $\mathrm{N}\left[0, (\sigma_y^i)^2\right]$.

The contribution of the CPUE data to the negative log-likelihood function (after removal of constants) is then given by:

$$-lnL^{CPUE} = \sum_i \sum_y \left[ln(\sigma_y^i) + (\epsilon_y^i)^2/(2(\sigma_y^i)^2)\right] \tag{4.28}$$

where σ_y^i is the standard deviation of the residuals for the logarithms of index i in years y.

In the case of the more recent GLM-standardised species-disaggregated CPUE series, the catchability coefficient q^i for biomass index i is estimated by its maximum likelihood value, which in the more general case of heteroscedastic residuals is given by:

$$ln\hat{q}^i = \frac{\sum_y (lnI_y^i - ln\hat{B}_{fy}^{\exp})/(\sigma_y^i)^2}{\sum_y 1/(\sigma_y^i)^2} \tag{4.29}$$

For the historical species-combined ICSEAF CPUE series, more complicated assumptions are made, which are outlined in Section 4.3.1.1.

To avoid an unrealistic weight for these CPUE data (i.e. very small σ_y^is), a year-independent σ^i is estimated in the model fitting procedure for each series, with a lower bound of 0.25 for the historical ICSEAF CPUE series and one of 0.15 for the recent GLM-standardised CPUE series.

4.3.1.1 Historical ICSEAF CPUE series

Catches from before 1978 are species-aggregated, and consequently the ICSEAF CPUE series based on these catches are too. In this case, $\hat{I}_y^i$ is derived by assuming two types of fishing zones on each coast:

z1) a shallow-water zone, corresponding to *M. capensis* only, and

z2) a mixed zone, where both *M. capensis* and *M. paradoxus* were fished.

The total catch of hake of both species by fleet f in year y ($C_{BS,f,y}$) can be written as:

$$C_{BS,f,y} = C_{cap,f,y}^{z1} + C_{cap,f,y}^{z2} + C_{par,f,y} \tag{4.30}$$

where

$C_{cap,f,y}^{z1}$ is the *M. capensis* catch by fleet f in year y in the *M. capensis* only zone (z1),
$C_{cap,f,y}^{z2}$ is the *M. capensis* catch by fleet f in year y in the mixed zone (z2), and
$C_{par,f,y}$ is the *M. paradoxus* catch by fleet f in year y in the mixed zone.

Catch rate is assumed to be proportional to exploitable biomass. Furthermore, let γ be the proportion of the *M. capensis* exploitable biomass in the mixed zone, given by:

$$\gamma = B_{cap,f,y}^{exp,z2}/B_{cap,f,y}^{\exp} \tag{4.31}$$

In the interest of simplicity, γ is assumed to be time-invariant. Let E_{fy}^i be the fishing effort in zone i and $E_{fy} = \sum_i E_{fy}^i$ the total fishing effort across the two zones by fleet f in year y. Define ψ_{fy} as the proportion of the effort of fleet f in the mixed zone in year y, given by:

$$\psi_{fy} = E_{fy}^{z2}/E_{fy} \tag{4.32}$$

Then the catches for each zone can be written as:

$$C^{z1}_{cap,f,y} = q^{i,z1}_{cap} B^{\text{exp},z1}_{cap,f,y} E^{z1}_{fy} = q^{i,z1}_{cap}(1-\gamma) B^{\text{exp}}_{cap,f,y}(1-\psi_{fy}) E_{fy} \tag{4.33}$$

$$C^{z2}_{cap,f,y} = q^{i,z2}_{cap} B^{\text{exp},z2}_{cap,f,y} E^{z2}_{fy} = q^{i,z2}_{cap}\gamma B^{\text{exp}}_{cap,f,y}\psi_{fy} E_{fy} \tag{4.34}$$

$$C_{par,f,y} = q^{i}_{par} B^{\text{exp}}_{par,f,y} E^{z2}_{fy} = q^{i}_{par} B^{\text{exp}}_{par,f,y}\psi_{fy} E_{fy} \tag{4.35}$$

where q^{i,z_i}_{cap} is the catchability for *M. capensis* for zone z_i on coast i, and q^{i}_{par} is the catchability for *M. paradoxus* on coast i.

It follows that:

$$C_{cap,f,y} = B^{\text{exp}}_{cap,f,y} E_{f,y}\left[q^{i,z1}_{cap}(1-\gamma)(1-\psi_{fy}) + q^{i,z2}_{cap}\gamma\psi_{fy}\right] \tag{4.36}$$

and

$$C_{par,f,y} = B^{\text{exp}}_{par,f,y} E_{f,y} q^{i}_{par}\psi_{fy} \tag{4.37}$$

ψ_{fy} can be solved for from Equations 4.36 and 4.37:

$$\psi_{fy} = \frac{q^{i,z1}_{cap}(1-\gamma)}{\frac{C_{cap,f,y} B^{\text{exp}}_{par,f,y} q^{i}_{par}}{B^{\text{exp}}_{cap,f,y} C_{par,f,y}} - q^{i,z2}_{cap}\gamma + q^{i,z1}_{cap}(1-\gamma)} \tag{4.38}$$

and finally, the model-estimated biomass indices are:

$$\hat{I}^{i}_{y} = \frac{C_{fy}}{E_{fy}} = \frac{C_{fy} B^{\text{exp}}_{par,f,y} q^{i}_{par}\psi_{fy}}{C_{par,f,y}} \tag{4.39}$$

For consistency, the q's for each species and zone are forced to be in the same proportion for the West Coast and South Coast:

$$q^{SC}_{s} = r q^{WC}_{s} \tag{4.40}$$

where $q^{WC,z1}_{cap}$, $q^{WC,z2}_{cap}$, q^{WC}_{par}, r and γ are estimated directly in the fitting procedure.

4.3.2 Survey biomass data

Biomass estimates from the research surveys (see Tables 3.3a and 3.3b) are treated as relative abundance indices in a similar manner to the GLM species-disaggregated CPUE series in Equations 4.27 and 4.28, with the biomass available to survey i, $B^{\text{surv},i}_{sy}$ (Equation 4.22), replacing the exploitable $B^{\text{exp},i}_{sfy}$. The associated σ^{i}_{y} for Equation 4.28 is taken to be given by the survey CVs of the biomass indices (see Tables 3.3a and 3.3b). However, since these estimates are unlikely to include all sources of variability, an additional variance parameter, $(\sigma_A)^2$, is estimated in the model to avoid unrealistically high weight being accorded to these indices in the likelihood. Hence Equation 4.28 is adjusted to:

$$-lnL^{\text{survey}} = \sum_{i}\sum_{y}\left[ln\left(\sqrt{(\sigma^{i}_{y})^2 + (\sigma_A)^2} + \frac{(\epsilon^{i}_{y})^2}{2\left((\sigma^{i}_{y})^2 + (\sigma_A)^2\right)}\right)\right] \tag{4.41}$$

where $(\sigma_A)^2$ is constrained to be greater than zero.

From 2003, new trawl gear was phased in on the *Africana*. A different length-specific selectivity is estimated for the new and old gears (see Section 4.2.9), and calibration estimates are available from calibration experiments conducted between the new and old gears (Smith *et al.* 2013):

$(q_{new}/q_{old})^{capensis} = 0.652$ with SE=0.073
$(q_{new}/q_{old})^{paradoxus} = 0.883$ with SE=0.082

The following contribution is consequently added as a penalty to the negative log-likelihood:

$$-lnL^{new\ gear} = (lnq_{new} - lnq_{old} - \Delta lnq)^2 / 2\sigma^2_{\Delta lnq} \tag{4.42}$$

4.3.3 Commercial proportions-at-length

The catches-at-length from the West Coast and South Coast offshore fleet, as well as the West Coast longline fleet, were not by disaggregated by species and are assumed to apply to the model-estimated proportions-at-length for both species combined. The catches-at-length from the South Coast inshore and longline fleets are assumed to consist of *M. capensis* only.

The model-estimated catches-at-length for each year are computed from the population sizes at the beginning of July:

$$C_{slfy} = \sum_m S_{slfy} F_{sfy} \sum_{a=0}^{a_m} A_{s,a,l} N_{say,m=7} \frac{(1 - e^{Z_{saym}})}{Z_{saym}} \tag{4.43}$$

with the species combined catches-at-length given by $C_{lfy} = \sum_s C_{slfy}$.

The species-aggregated (or disaggregated) model-predicted proportions-at-length are then given by:

$$\hat{p}_{(s)lfy} = C_{(s)lfy} / \sum_{l'} C_{(s)l'fy} \tag{4.44}$$

The contribution of the proportion-at-length to the negative of the log-likelihood function assumes the Punt and Kennedy (1997) error distribution form given by:

$$-lnL^{length} = 0.1 \sum_y \sum_l \sum_f \left[ln\left(\sigma_{len,f} / \sqrt{p^{obs}_{(s)lfy}}\right) + p^{obs}_{(s)lfy} \left(lnp^{obs}_{(s)lfy} - ln\hat{p}_{(s)lfy}\right)^2 / 2(\sigma_{len,f})^2 \right] \tag{4.45}$$

where $p^{obs}_{(s)lfy}$ is the observed species-aggregated (or disaggregated) proportion-at-length from fleet f, and $\sigma_{len,f}$ is the standard deviation associated with the proportion-at-length data, which is calculated in the fitting procedure by:

$$\hat{\sigma}_{len,f} = \sqrt{\sum_y \sum_l p^{obs}_{(s)lfy} \left(lnp^{obs}_{(s)lfy} - ln\hat{p}_{(s)lfy}\right)^2 / \sum_y \sum_l 1} \tag{4.46}$$

The multiplicative factor of 0.1 in Equation 4.45 was implemented by Rademeyer and Butterworth (2014b) to downweight the likelihood contribution in light of correlation between proportions in adjacent length groups. The value of 0.1 was based roughly on the ratio of the number of age classes to the number of length groups in the model, as a coarse approach to allow for this correlation. The same weighting has been assumed for the predation model.

The summation over length l in Equation 4.45 is taken from length l_{minus} (considered as a minus group) to l_{plus} (a plus group). The fleet-specific lengths for the minus- and plus-groups are provided in Table 4.6 and are chosen so that the majority of observations fall between l_{minus} and l_{plus}.

4.3.4 Survey proportions-at-length

The observed, species-disaggregated, survey proportions-at-length (Tables 3.4c to 3.4h) have been weighted by depth stratum according to the method of "Sen 2" of Appendix 3.A. The model-predicted proportions-at-length are calculated as follows:

$$\hat{p}_{sly}^{\text{surv},i} = \frac{\sum_a S_{sl}^{\text{surv},i} A_{sal} N_{say,m_i}}{\sum_{l'} \sum_a S_{sl'}^{\text{surv},i} A_{sal'} N_{say,m_i}} \tag{4.47}$$

where the month index m_i is again taken to be 1 for the summer surveys, 4 for the autumn surveys, 7 for the winter surveys and 10 for the spring surveys. These proportions are incorporated into the negative log-likelihood in a similar manner to the commercial catches-at-age (Equation 4.45).

4.3.5 Stock-recruitment residuals

The stock-recruitment residuals, ζ_{sy}, are estimated for the years 1985 to 2013, made possible by the availability of catch-at-length data for these years, which give some indication of the length- (and thus the age-) structure of the population. For all other years the recruitment is assumed to be exactly as specified by the stock-recruitment relationship. The stock-recruitment residuals are assumed to be log-normally distributed, and their contribution to the negative log-likelihood function is given by:

$$-lnL^{SR} = \sum_s \left[\sum_{y=1985}^{2013} \zeta_{sy}^2 / 2\sigma_R^2 + \left(\sum_{y=1985}^{2013} \zeta_{sy} \right)^2 / 0.01^2 \right] \tag{4.48}$$

where

ζ_{sy} is the recruitment residual for species s, and year y, estimated for the years 1985 to 2013, and
σ_R is the standard deviation of the log of the residuals, which is specified as described below.

σ_R measures the extent of variability in recruitment. Recruitment for the last five years of the model are forced to lie closer to the stock-recruitment curve by having the σ_R decrease linearly from 0.45 to 0.1 over that period, to increase estimation stability given few cohorts present in the catches to inform on recruitment strengths for these years.

4.3.6 Catch penalty

The observed catches in year y are assumed to be split equally amongst the 12 months of that year. The hybrid method (Appendix 4.A) used to calculate the fishing mortalities for the model-predicted catches allows the model the flexibility to not match the observed catches, but at the cost of a penalty to the negative log-likelihood:

$$-lnL+ = \sum_{s,f} \left(ln\left(C_{sfy}^{obs}\right) - ln\left(\sum_m C_{sfym} \right) \right)^2 / \left(2\left(0.1\right)^2 \right) \tag{4.49}$$

where C^{obs}_{sfy} is the observed catch for fishing fleet f in year y, and C_{sfym} is the model-predicted catch in month m of year y (Equation 4.20).

4.4 Estimable parameters

The primary parameters estimated for the population dynamics of the non-predation component of the model are the species-specific pre-exploitation spawning biomass K^{sp}_s and the stock-recruitment residuals. The "steepness" (h_s) of the stock-recruitment curve is pre-specified in the base case model and only estimated in a sensitivity run.

For the fits to the CPUE data, the standard deviations σ^i for the residuals of each CPUE series (the historical ICSEAF as well as the GLM-standardised series) and the additional variance $(\sigma^i_A)^2$ for the survey abundance series are treated as estimable parameters in the minimisation process. Further, for the historical CPUE series, $q^{WC,z1}_{cap}$, $q^{WC,z2}_{cap}$, q^{WC}_{par}, r and γ are estimated.

Parameters for the survey selectivities are estimated for the seven lengths specified for each species and survey type (West Coast winter, West Coast summer, South Coast spring, South Coast autumn). Separate selectivities are estimated for the new gear, but only for the first five lengths since the same selectivity as the old gear is assumed for older fish. Table 4.5 provides the details and number of estimable parameters for the commercial selectivity.

Table 4.7 provides a summary of the estimable parameters for the non-predation component of the model.

Table 4.1: Female maturity-at-length ogive (Equation 4.12) parameter estimates (Singh *et al.* 2011). These values are assumed to apply to all hake in the hake predation model presented in this thesis.

Species	l_{50} (cm)	Δ (cm)
M. paradoxus	41.53	2.98
M. capensis	53.83	10.14

Table 4.2: The Rademeyer and Butterworth (2014b) reference case estimates for the von Bertalanffy growth curve parameters (Equation 4.14), and the variance parameters (Equation 4.15). These values have been input into the predation model. Note that L_5 is the length at age 5, the estimation of which Rademeyer and Butterworth (2014b) found to be more stable than the estimation of L_∞. Furthermore, Rademeyer and Butterworth (2014b) estimate $\sigma^A_{s,1}$ and $\sigma^A_{s,14}$ instead of α^A_s and β^A_s from Equation 4.15. The gender-specific estimates from Rademeyer and Butterworth (2014b) have been averaged to obtain the values listed in the Table, so that effectively a 50:50 sex ratio is being assumed.

	Growth curve parameters			Variance parameters		
Species	L_5 (cm)	κ*	t_0	$\sigma^A_{s,0}$	$\sigma^A_{s,1}$	$\sigma^A_{s,14}$
M. paradoxus	48.42	$5.046e^{-5}$	-0.8660	1.382	4.368	10.311
M. capensis	51.24	$5.012e^{-5}$	-0.8185	2.545	4.677	6.659

*The low values estimated for κ reflect a near linear straight line through zero length at t_0 to L_5 at age 5.

Table 4.3: Length-weight relationship estimates. The sex-specific estimates (Singh 2013) were utilised in the Rademeyer and Butterworth (2014b) model, while the sex-aggregated estimates were used in Rademeyer *et al.* (2008b) and also in the predation model presented in this thesis.

	α (g/cm^β)	β	Source
M. paradoxus:			
Males:	0.00775	2.977	Singh (2013)
Females:	0.00570	3.071	Singh (2013)
Sex-aggregated:	0.0062	3.046	Punt and Leslie (1991)
M. capensis:			
Males:	0.00675	3.044	Singh (2013)
Females:	0.00595	3.075	Singh (2013)
Sex-aggregated:	0.0050	3.113	Punt and Leslie (1991)

Table 4.4: Lengths (in cm) at which survey selectivity is estimated directly. Note that since selectivity is standardised so that the maximum is one, selectivities need to be estimated at only 7 of the of the 8 lengths listed in the Table.

	Survey	Lengths (cm)							
M. paradoxus	West Coast summer	13	18	23	28	32	37	42	47
	West Coast winter	13	18	24	29	35	40	46	51
	South Coast spring	21	26	30	35	39	44	48	53
	South Coast autumn	21	26	31	36	42	47	52	65
M. capensis	West Coast summer	13	20	26	33	39	46	52	59
	West Coast winter	13	17	21	30	40	47	54	61
	South Coast spring	13	19	28	38	46	54	63	71
	South Coast autumn	13	19	28	36	44	52	61	69

Table 4.5: Details for the commercial selectivity-at-length for each fleet and species combination and the number of estimable parameters. This Table has been adapted from Rademeyer and Butterworth (2014b).

	M. paradoxus		***M. capensis***	
	No. est. param.	Comments	No. est. param.	Comments
1. West Coast offshore				
1917-1976	0	average between 77-84 and 93-2013 period	0	average between 77-84 and 93-2013 period
1977-1984	3	double logistic (σ_{left}, σ_{right} and l_{est})	0	as 93-2013, but σ_{left} same difference as for *M. paradoxus* between 77-84 and 93-2013
1985-1992	0	linear change between 84 and 93 selectivity	0	linear change between 84 and 93 selectivity
1993-2013	3	double logistic (σ_{left}, σ_{right} and l_{est})	0	Based on inshore selectivity: $l_{est} = l_{est}$(inshore)+5, $\sigma_{left} = \sigma_{left}$(inshore) and $\sigma_{right} = 3 * \sigma_{right}$(inshore)
2. South Coast offshore				
1917-1976	0	average between 77-84 and 93-2013 period	0	average between 77-84 and 93-2013 period
1977-1984	0	same as 1993-2013	0	as 93-2013, but σ_{left} same difference as for *M. paradoxus* between 77-84 and 93-2013
1985-1992	0	linear change between 84 and 93 selectivity	0	linear change between 84 and 93 selectivity
1993-2013	3	double logistic (σ_{left}, σ_{right} and l_{est})	0	Based on inshore selectivity: $l_{est} = l_{est}$(inshore)+5, $\sigma_{left} = \sigma_{left}$(inshore) and $\sigma_{right} = 3 * \sigma_{right}$(inshore)
3. South Coast inshore	-	-	3	double logistic (σ_{left}, σ_{right} and l_{est})
4. West Coast longline*	3	double logistic (σ_{left}, σ_{right} and l_{est})	-	same as *M. paradoxus*
5. South Coast longline*	3	double logistic (σ_{left}, σ_{right} and l_{est})	-	same as *M. paradoxus*
6. South Coast handline	-	-	0	same as South Coast longline

* The Rademeyer and Butterworth (2014b) model assumes three periods of selectivity for the longline fleet, and estimates separate selectivities for *M. paradoxus* and *M. capensis*.

Table 4.6: Minus- and plus-groups taken for the surveys and commercial proportion-at-length data, in terms of length in cm.

SURVEY DATA Survey	Species	Minus	Plus
West Coast summer	*M. paradoxus*	13	47
	M. capensis	13	59
West Coast winter	*M. paradoxus*	13	51
	M. capensis	13	61
South Coast spring	*M. paradoxus*	21	53
	M. capensis	13	71
South Coast autumn	*M. paradoxus*	21	65
	M. capensis	13	69
COMMERCIAL DATA Fleet	Species	Minus	Plus
West Coast offshore trawl	species combined	23	65
South Coast offshore trawl	species combined	27	75
South Coast inshore trawl	*M. capensis*	27	65
West Coast longline	species combined	45	91
South Coast longline	*M. capensis*	45	91

Table 4.7: Parameters estimated in the model fitting procedure, excluding all predation-related parameters from Chapter 5. Note that the base case does not fit the stock-recruitment parameters.

	No. of params	**Parameters estimated**	**Bounds enforced**
K^{sp}	2	$ln(K^{sp}_{cap})$ and $ln(K^{sp}_{par})$	(2; 15)
Recruitment: Beverton Holt	(2)	h_{cap} and h_{par}	h (0.5; 0.98)
Recruitment: modified Ricker*	(4)	h_{cap}, h_{par}, $\gamma_{R,cap}$ and $\gamma_{R,par}$	h (0.2; 1.5), γ_R (0,10)
Additional survey variance	2	$\sigma_{A,cap}$ and $\sigma_{A,par}$	(0,0.5)
Recruitment residuals	58	$\zeta_{cap,1985-2013}$ and $\zeta_{par,1985-2013}$	(-5; 5)
σ_{CPUE}	6	one for each series	ICSEAF: (0.25; 1) and GLM: (0.15; 1)
ICSEAF CPUE	5	$q^{WC,z1}_{cap}$, $q^{WC,z2}_{cap}$, q^{WC}_{par}, r and γ	q (0;30), r (0;10) and γ: (0; 0.95)
Survey selectivity	86	Parameters for each specified length (Table 4.4)	(0;25)
Commercial selectivity	18	Parameters as per Table 4.5	(0;18)
Total (excl. stock-recruitment)	**177**		

*See Equation 6.1 of Chapter 6.

Appendices

4.A The hybrid method for calculating fishing mortality

4.A.1 Introduction

The use of Pope's approximation for catches carries with it the problem that catches may exceed model-predicted population sizes. In ADMB, the *posfun* function may be utilised to prevent the population from going negative, but this may also create difficulties in the minimisation process as a result of the high penalties that often arise from use of the *posfun* function. During discussions of ADMB convergence issues at the 2013 International Stock Assessment Workshop (Smith *et al.* 2013), it was recommended that use of the *posfun* function should be avoided as much as possible. Instead, the Baranov catch formulation should be used, since under that formulation $N_{y+1,a+1} = N_{y,a}e^{-(M_a+F)}$, i.e. $N_{y+1,a+1} > 0$ at all times.

In the Baranov formulation for the catch equation, the model-predicted catches (by mass) are given by:

$$C^{mod} = \sum_a FS_aN_aw_a\frac{1-e^{-(M_a+FS_a)}}{M_a+FS_a}$$

Since the fishing mortality F cannot be calculated explicitly, it can either be treated as an estimable parameter, or obtained using a Newton-Raphson algorithm with a fixed number of iterations.

4.A.2 Method 1: Solving F for one fleet (Newton-Raphson)

For simplicity, unnecessary subscripts have been omitted, and the predation mortality is not included. In practice indices for year, species etc. would need to be retained where applicable. Define the function $g(F)$:

$$g(F) = C^{mod} - C^{obs} = \sum_a FS_aN_aw_a\frac{1-e^{-(M_a+FS_a)}}{M_a+FS_a} - C^{obs} \tag{4.A.19}$$

Values of F are needed for which $g(F) = 0$. Take C^{obs} as a starting value, i.e. $F_1 = C^{obs}$, and implement Newton-Raphson to find the roots:

$$F_{n+1} = F_n - \frac{g(F_n)}{g'(F_n)} \tag{4.A.20}$$

where

$$g'(F) = \sum_a S_aN_aw_a\frac{1-e^{-(M_a+FS_a)}}{M_a+FS_a} + \sum_a FS_aN_aw_a\frac{e^{-(M_a+FS_a)}}{M_a+FS_a} - \sum_a FS_aN_aw_a\frac{1-e^{-(M_a+FS_a)}}{(M_a+FS_a)^2} \tag{4.A.21}$$

It is important that a fixed number of iterations is used in the minimisation process (because of the use of ADMB, which requires differentiable functions), and generally < 5 iterations are required to obtain an accurate answer.

Lastly, a penalty is added to the likelihood for when catches are too large. In such a case $g(F) = 0$ will have no real solution (i.e. there is no F such that $C^{obs} = F\frac{1-e^{-(M+F)}}{M+F}$) and the closest possible solution will be found. Since C^{mod} will not match C^{obs}, this additional penalty added is:

$$-lnL+ = \left(ln(C^{obs}) - ln(C^{mod})\right)/(2\sigma_C^2) \tag{4.A.22}$$

4.A.3 Method 2: Solving F_f for several fleets — the hybrid method

The approach above is straightforward to implement when there is only one fishing fleet. For several fleets, a Newton-Raphson approach for several variables would need to be used, which would quickly become very complicated. Below is a description of the method provided by A. Punt (*pers. comm.*) that solves for F when there are multiple fleets. Again, subscripts for year, month, species etc would need to be added in practice.

Step 1: Initial guess

Let $\tilde{F}_f^1$ be an initial guess for F_f:

$$\tilde{F}_f^1 = C_f^{obs} / \left(\sum_a N_a S_{f,a} w_a + C_f^{obs} \right) \tag{4.A.23}$$

The actual starting estimate for F_f is derived from $\tilde{F}_f^1$ as follows:

$$F_f^1 = -ln\left(1 - \left[\tilde{F}_f^1 \left(\frac{1}{1+e^{30(\tilde{F}_f^1 - 0.95)}}\right) + 0.95\left(1 - \frac{1}{1+e^{30(\tilde{F}_f^1 - 0.95)}}\right)\right]\right) \tag{4.A.24}$$

This formulation serves to put an upper limit on F_f^1. The choice of 0.95 determines this upper limit, since as $\tilde{F}_f^1 \to \infty$, $F_f^1 \to -ln(1-0.95) \approx 3$, as illustrated in Figure 4.A.1 below.

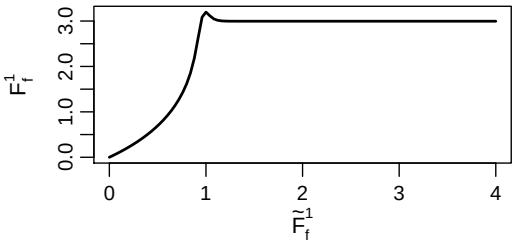

Figure 4.A.1: Starting estimate F_f^1 as a function of $\tilde{F}_f^1$

Step 2: Compute the model-predicted catches given F_f^i and M_a

Let $Z_a^i = M_a + \sum_f F_f^i S_{f,a}$. Then the model-predicted catches are given by:

$$C_f^{mod} = \sum_a F_f^i S_{f,a} N_a w_a \frac{1 - e^{-Z_a^i}}{Z_a^i} \tag{4.A.25}$$

Step 3: Compute an adjustment factor, and adjust Z

An adjustment factor A^i is computed so that if the model-predicted catches are too small ($C^{obs} > C^{mod}$), then $A^i > 1$, and if they are too large then $A^i < 1$.

$$A^i = \left(\sum_f C_f^{obs} \right) / \left(\sum_f C_f^{mod} \right) \tag{4.A.26}$$

The F component of the mortality is then scaled accordingly:

$$Z_a^i = M_a + \sum_f (A^i F_f^i) S_{f,a} \tag{4.A.27}$$

Step 4: Find F_f^{i+1} for next iteration

The next estimate for F_f is given by:

$$\tilde{F}_f^{i+1} = C_f^{obs} / \left(\sum_a S_{f,a} N_a w_a \frac{1 - e^{-Z_a^i}}{Z_a^i} \right) \tag{4.A.28}$$

Note the congruence between Equation 4.A.28 and Equation 4.A.25 with F_f^i as the subject of the formula. To obtain the next iterative value for F, the following formulation is used so that there is an upper limit on F:

$$F_f^{i+1} = \tilde{F}_f^{i+1} \left(\frac{1}{1 + e^{30(\tilde{F}_f^{i+1} - 0.95F^{max})}} \right) + F^{max} \left(1 - \frac{1}{1 + e^{30(\tilde{F}_f^{i+1} - 0.95F^{max})}} \right) \tag{4.A.29}$$

In other words when $\tilde{F}_f^{i+1} < 0.95F^{max}$, F_f^{i+1} has a near to linear (1:1) relationship with $\tilde{F}_f^{i+1}$. As $\tilde{F}_f^{i+1}$ approaches $0.95F^{max}$, the F^{max} contribution in Equation 4.A.29 starts to dominate and $F_f^{i+1} \to F^{max}$, as illustrated in Figure 4.A.2.

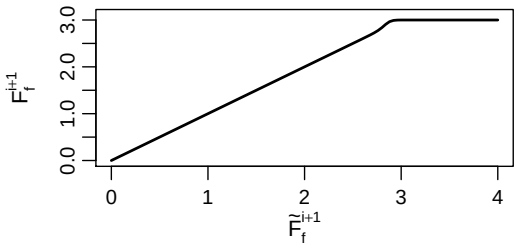

Figure 4.A.2: F_f^{i+1} as a function of $\tilde{F}_f^{i+1}$ in the iterative process.

Step 5: Last iteration

Step 2 - Step 4 are repeated until the last iteration is reached (e.g. iteration 5). At the last iteration, Step 2 - Step 4 are not followed, and instead the model-predicted catch and mid-year biomass are computed based on the final F obtained.

Chapter 5

The hake predation model

5.1 Introduction

This Chapter presents the details and equations for the methods used to incorporate the additional hake predation and cannibalism components in the model presented in Chapter 4.

The earliest version of the hake predation model implemented the same methods as Punt and Butterworth (1995), which specify the daily ration as an input to the model and split this ration into a hake (by prey age) and non-hake component based on a combination of a predator-prey preference function and model estimates of the hake population sizes.

This early version of the predation model was presented to the International Stock Assessment Workshop[1] (IWS) for the first time in 2011 (Smith *et al.* 2011), and later versions were reviewed in 2013, 2014 and 2015 (Smith *et al.* 2013, Dunn *et al.* 2014, Dunn *et al.* 2015). Much of the development of the model took place as a consequence of recommendations made by the international panel at these workshops. Appendix 5.A provides a list of all the recommendations made by these panels on this topic over the years, but probably the most influential recommendations arose from IWS 2013, primarily in response to issues with instability that were being experienced with the predation model at the time. First, the panel at that time recommended that the daily ration should not be pre-specified as an input, but rather that the model should be given the flexibility to estimate this daily ration, which could then be compared to what was considered biologically realistic. This recommendation was made in light of the substantial uncertainty concerning what these daily rations should be in the first place, and issues of instability in the estimation process that arose when the daily ration (and thus to an extent the hake mortality rates) was pre-specified. A second important recommendation was to implement a Baranov formulation of the catch equation (the model at the time used Pope's approximation), since this approach does not allow for catches to exceed the population size and produces greater stability in the estimation process. Lastly, the panel recommended the implementation of some of the methods of Kinzey and Punt (2009), which led, amongst other changes, to a re-parameterisation of the feeding functional response to simplify the equilibrium setup, and to the introduction of an "Other prey" component to the model.

[1] More details about this workshop are provided in Appendix 5.A.

5.2 Basic dynamics

Chapter 4 provides the details for the non-predation aspects of this model. For the reader's ease, the essential basic population dynamic equations have been repeated here.

The number of hake of species s and age $\tilde{a}$ months in month m of year y is given by:

$$\widetilde{N}_{s,\tilde{a}+1,y,m+1} = \widetilde{N}_{s,\tilde{a},y,m} e^{-Z_{saym}} \tag{5.1}$$

Even though the model tracks the population numbers by age in months, it is assumed that hake of the same age in years will experience the same mortality (i.e. Z_{saym} is a function of age in years). This assumption may not be entirely accurate, but the loss of accuracy here would likely be far out-weighed by the additional computational difficulties that arise when assuming a mortality that depends on age in months. As described in Chapter 4, the total mortality is given by:

$$Z_{saym} = M_s^{basal}/12 + P_{saym} + \sum_f S_{saf} F_{sfym} \tag{5.2}$$

where

$\sum_f S_{saf} F_{sfym}$	is the total fishing mortality in month m of year y,
P_{saym}	is the mortality due to predation by other hake, and
M_s^{basal}	is a basal natural mortality rate for all sources other than predation by hake and fishing mortality.

The value of M_s^{basal} is assumed to be age-independent[2] and is fixed on input, with sensitivity tested to the value assumed (see Section 6.5).

5.3 Predation dynamics

This section describes how the predation mortality rate, P_{saym}, is developed. In order to distinguish between hake predator and prey species in the equations that follow, the superscripts s_p and a_p are used for the predators, while the subscripts s and a are used for the prey. Thus $N_{ym}^{s_p a_p}$ denotes the number of predators of species s_p and age a_p, and N_{saym} the number of prey of species s and age a in month m of year y.

5.3.1 Hake prey

The following equations are based in part on those given in Kinzey and Punt (2009), with several adjustments. Let $V_{saym}^{s_p a_p}$ be the mortality rate of hake prey of species s and age a due to hake predators of species s_p and age a_p. Then the total predation rate on these particular prey is:

$$P_{saym} = \sum_{s_p, a_p} V_{saym}^{s_p a_p} \tag{5.3}$$

[2] Age-independence is assumed in the interest of simplicity, but sensitivity to this is tested (see Chapter 6).

where $V_{saym}^{s_p a_p}$ is modelled here by a Holling Type II functional form[3]:

$$V_{saym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{5.4}$$

Here

- $\breve{N}_{ym}^{s_p a_p}$ is the number of hake predators of species s_p and age a_p in month m of year y, relative to the equilibrium maximum age group (see Equation 5.20),
- $\Phi_{sym}^{s_p a_p}$ is a relative measure of the abundance of hake prey of species s available to hake predators of species s_p and age a_p in month m of year y (see Equation 5.21),
- $\gamma_{sa}^{s_p a_p}$ is a preference function modelling the preference that a hake predator of species s_p and age a_p exhibits for hake prey of species s and age a (see Equation 5.13),
- $\theta^{s_p a_p}$ is a function allowing for additional flexibility in the extent to which predation rates change with the age of the hake predator (see Equation 5.15),
- $O_{other}^{s_p a_p}$ is the population size in numbers of other (non-hake) prey available to hake predators of species s_p and age a_p, which is assumed to be time-invariant (see Section 5.3.2), and
- $\nu_s^{s_p}$, $\tilde{\nu}_s^{s_p}$ and $\tilde{\nu}_{other}^{s_p}$ are estimable parameters.

The number of hake prey of species s and age a consumed in month m of year y by predators of species s_p and age a_p is given by:

$$E_{saym}^{s_p a_p} = V_{saym}^{s_p a_p} N_{saym} \frac{\left(1 - e^{-Z_{saym}}\right)}{Z_{saym}} \tag{5.5}$$

Finally, the mass of hake of species s consumed in year y by predators of species s_p and age a_p is given by:

$$Q_{sym}^{s_p a_p} = V_{saym}^{s_p a_p} \left(\sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}ym} w_{s\tilde{a}} \right) \frac{\left(1 - e^{-Z_{saym}}\right)}{Z_{saym}} \tag{5.6}$$

As explained in Chapter 4, $\sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}ym} w_{s\tilde{a}}$ is the total weight of prey taking their individual weight by age in months into account.

5.3.2 Other prey

The approach used for setting up the hake prey dynamics has been mirrored in setting up the equations for the amount of other prey consumed. Recall that $O_{other}^{s_p a_p}$ is the number of non-hake prey available to hake predators of species s_p and age a_p. Let the total mortality rate for other prey be given by:

$$Z_{other,ym}^{s_p a_p} = M_{other}^{basal}/12 + P_{other,ym} \tag{5.7}$$

where

- M_{other}^{basal} is the basal mortality rate for the other prey, fixed at 0.2 p.a., and
- $P_{other,ym}$ is the predation mortality on other prey due to hake predators, given by:

$$P_{saym} = \sum_{s_p, a_p} V_{other,ym}^{s_p a_p} \tag{5.8}$$

[3] Equation 5.4 is in fact a re-parameterised version of the basic Holling Type II form. Further details of the relationship between the two are given in Section 5.3.5.1.

$V^{s_p a_p}_{other,ym}$ is the mortality of other prey due to hake predators of species s_p and age a_p in month m of year y, also modelled by a Holling Type II functional form[4]:

$$V^{s_p a_p}_{other,ym} = \breve{N}^{s_p a_p}_{ym} \frac{\nu^{s_p}_{other} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}^{s_p}_s \Phi^{s_p a_p}_{sym} + \tilde{\nu}^{s_p}_{other} O^{s_p a_p}_{other}} \tag{5.9}$$

The mass of other prey consumed in year y by predators of species s_p and age a_p is then given by:

$$Q^{s_p a_p}_{other,ym} = V^{s_p a_p}_{other,ym} \tilde{O}^{s_p,a_p}_{other} \frac{\left(1 - e^{-Z_{other,ym}}\right)}{Z_{other,ym}} \tag{5.10}$$

$\tilde{O}^{s_p,a_p}_{other}$ is a measure of the **mass** of the other prey available to a hake predator of species s_p.

5.3.2.1 Other prey in numbers

Since O^{s_p,a_p}_{other} is multiplied by the estimable parameter $\tilde{\nu}^{s_p}_{other}$ in Equations 5.4 and 5.9, the magnitude of O^{s_p,a_p}_{other} does not matter, only how it varies relative to predator age a_p. O^{s_p,a_p}_{other} is consequently modelled by a simple exponential equation:

$$O^{s_p,a_p}_{other} = e^{-(o^{s_p})a_p} \tag{5.11}$$

where o^{s_p} is an estimable parameter that can take on positive or negative values.

5.3.2.2 Other prey by mass

The mass of other prey available to a hake predator of species s_p and age a_p is taken to be a multiple of the other prey by numbers:

$$\tilde{O}^{s_p,a_p}_{other} = o^{s_p}_w O^{s_p a_p}_{other} \tag{5.12}$$

where $o^{s_p}_w$ is an estimable scaling parameter.

5.3.3 Preference function

The preference function for hake predators on hake prey is modelled using a gamma function, as in Kinzey and Punt (2009):

$$\gamma^{s_p a_p}_{sa} = \left(G^{s_p a_p}_{sa} / \tilde{G}^{s_p}_s\right)^{\alpha^{s_p}-1} exp\left[-\left(G^{s_p a_p}_{sa} - \tilde{G}^{s_p}_s\right)/\beta^{s_p}\right] \tag{5.13}$$

where

$G^{s_p a_p}_{sa}$	is the logarithm of the ratio of the expected length of a hake predator of species s_p and age a_p to that of a hake prey of species s and age a,
$\tilde{G}^{s_p}_s = (\alpha^{s_p} - 1)\beta^{s_p}$	is the value of $G^{s_p a_p}_{sa}$ at which predator selectivity is at a maximum, and
α^{s_p} and β^{s_p}	are estimable parameters.

In practice, $\tilde{G}^{s_p}_s$ is treated as the estimable parameter in the place of β^{s_p}, since $\tilde{G}^{s_p}_s$ (the peak of the preference function) is a more biologically meaningful quantity. Furthermore a prey-specific $\tilde{G}^{s_p}_s$ is estimated[5], since it is possible that the preference that *M. capensis* predators exhibit for *M. capensis* prey may peak at a different prey

[4]Similarly to Equation 5.4, Equation 5.9 is a re-parameterised version of the basic Holling Type II form. Further details are given in Section 5.3.5.1

[5]This prey-specificity applies only to *M. capensis* predators, since *M. paradoxis* is assumed not to eat *M. capensis*.

to predator size ratio than for *M. paradoxus* prey, given that the overlap between *M. capensis* predators and their prey differs between the two prey species. The preference function is normalised so that $\sum_{s,a} \gamma_{sa}^{s_p a_p} = 1$.

With the formulation of the preference function in Equation 5.13, difficulties can occasionally arise in the minimisation process if a sufficiently large α^{s_p} (i.e. a narrow gamma distribution) is estimated. At such times, it is possible for the distribution of $\gamma_{sa}^{s_p a_p}$ for a given predator age a_p to lie almost entirely *between* two prey ages, resulting in virtually zero preference for hake being exhibited by that predator age group. This issue was addressed by evaluating Equation 5.13 for prey ages a; $a + \frac{1}{12}$; $a + \frac{2}{12}$; ... ; $a + \frac{11}{12}$. The value of the preference function is then taken to be the average of the function evaluated at each of these 12 increments.

5.3.4 Theta function

The $\theta^{s_p a_p}$ function provides additional flexibility for varying predation rates with predator age. Kinzey and Punt (2009) introduce $\theta^{s_p a_p}$ in order to *reduce* predation as predator age increases (for example to allow for the fact that larger fish may focus less on feeding and growth, and more on reproducing). They use the form:

$$\theta^{s_p a_p} = 1 + \omega^{s_p} \tilde{\omega}^{s_p} / \left(a_p + \tilde{\omega}^{s_p}\right) \tag{5.14}$$

where ω^{s_p} and $\tilde{\omega}^{s_p}$ are estimable parameters. When this form was implemented in the hake predation model, it resulted in older fish not eating enough, so that some changes were made to allow $\theta^{s_p a_p}$ to increase with predator age, with the following form:

$$\theta^{s_p, a_p} = w^{s_p, a_p} \left[\frac{\omega^{s_p} + 5}{\omega^{s_p} + a_p}\right]^{\tilde{\omega}^{s_p}} \tag{5.15}$$

where w^{s_p, a_p} is the weight of a hake predator of species s_p and age a_p, and ω^{s_p} and $\tilde{\omega}^{s_p}$ are estimable parameters. The predator weight was included under the rationale that a predator is likely to eat more as it gets bigger.

5.3.5 Initial population setup

In order to obtain the pre-exploitation equilibrium structure, the total mortality values $Z_{say_0,m=1} = M_{sa}^{basal} + P_{s,a,y_0,m=1}$ are needed. However, to obtain $P_{s,a,y_0,m=1}$, the initial population structure is needed. To address this impasse, the formulation of Equations 5.4 and 5.9 was chosen so that the calculation of an initial structure was made possible using the methodology described below. Note that y_0 is the first year considered in the model, namely 1916, and $m = 1$ is the first month, January.

The approach used to obtain an initial population structure starts with the oldest hake predators and systematically moves to zero year old hake, computing predation rates along the way. The basic assumption is that hake of age 15 and above (the age plus-group) are too large to be preyed upon by other hake, i.e $P_{s,a_m,y_0,m=1} = 0$ for $a_m = 15$. Thus the total mortality rate for this age group at pre-exploitation equilibrium (i.e. zero fishing mortality) is $Z_{s,a_m,y_0,m=1} = M_{sa_m}^{basal}$, where the basal mortality rate is fixed on input. The number of 14 year old hake can then be calculated from the number of 15 year old hake: $N_{s,a_m-1,y_0,m=1} = N_{s,a_m,y_0,m=1} e^{Z_{s,a_m,y_0,m=1}}$. It is then assumed that the only hake predators for 14 year old hake are 15 years and older, so that $P_{s,a_m-1,y_0,m=1}$ can then be calculated from $N_{s,a_m,y_0,m=1}$, allowing $N_{s,a_m-2,y_0,m=1} = N_{s,a_m-1,y_0,m=1} e^{Z_{s,a_m-1,y_0,m=1}}$ to be determined, and so on. By re-parameterising the predation equations as in Equations 5.4 and 5.9, one can set

$N_{s,a_m,y_0,m=1} = 1$ initially, and once $N_{s,a,y_0,m=1}$ has been obtained for all a, the numbers can be scaled so that the spawning biomass equals the model-estimated parameter value.

5.3.5.1 Derivation of Equations 5.4 and 5.9

The formulation chosen for Equations 5.4 and 5.9 is to enable implementation of the approach above. To derive these equations, one starts from more fundamental Holling Type II parameterisations:

$$V_{saym}^{s_p a_p} = N_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\eta_s^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\eta}_s^{s_p} \sum_a N_{saym} \gamma_{sa}^{s_p a_p} + \tilde{\eta}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{5.16}$$

and

$$V_{other,ym}^{s_p a_p} = N_{ym}^{s_p a_p} \frac{\eta_{other}^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\eta}_s^{s_p} \sum_a N_{saym} \gamma_{sa}^{s_p a_p} + \tilde{\eta}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{5.17}$$

where

$N_{ym}^{s_p a_p}$	is the number of hake predator fish of species s_p and age a_p in month m of year y,
N_{saym}	is the number of hake prey fish of species s and age a in month m of year y,
$\eta_s^{s_p}$, $\tilde{\eta}_s^{s_p}$, $\eta_{other}^{s_p}$, $\tilde{\eta}_{other}^{s_p}$	are estimable parameters, and

the other parameters are as for Equations 5.4 and 5.9.

Equations 5.16 and 5.17 are then re-written so that at unexploited equilibrium the N_{say_0m} term is effectively removed from the denominator:

$$V_{saym}^{s_p a_p} = \frac{N_{ym}^{s_p a_p}}{N_{y_0,m=1}^{s_p a_{p,max}}} \gamma_{sa}^{s_p a_p} \frac{\left(\eta_s^{s_p} N_{y_0,m=1}^{s_p a_{p,max}}\right) \theta^{s_p a_p}}{1 + \sum_s \left(\tilde{\eta}_s^{s_p} \sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p} \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p}}{\sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p}}\right) + \tilde{\eta}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{5.18}$$

and

$$V_{other,ym}^{s_p a_p} = \frac{N_{ym}^{s_p a_p}}{N_{y_0,m=1}^{s_p a_{p,max}}} \frac{\left(\eta_{other}^{s_p} N_{y_0,m=1}^{s_p a_{p,max}}\right) \theta^{s_p a_p}}{1 + \sum_s \left(\tilde{\eta}_s^{s_p} \sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p} \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p}}{\sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p}}\right) + \tilde{\eta}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{5.19}$$

Defining

$$\breve{N}_{ym}^{s_p a_p} = \frac{N_{ym}^{s_p a_p}}{N_{y_0,m=1}^{s_p a_{p,max}}} \tag{5.20}$$

$$\Phi_{sym}^{s_p a_p} = \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p}}{\sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p}} \tag{5.21}$$

$$\nu_s^{s_p} = \eta_s^{s_p} N_{y_0,m=1}^{s_p a_{p,max}} \tag{5.22}$$

$$\nu_{other}^{s_p} = \eta_{other}^{s_p} N_{y_0,m=1}^{s_p a_{p,max}} \tag{5.23}$$

$$\tilde{\nu}_s^{s_p a_p} = \tilde{\eta}_s^{s_p} \sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p} \implies \tilde{\nu}_s^{s_p} \tag{5.24}$$

$$\tilde{\nu}_{other}^{s_p} = \tilde{\eta}_{other}^{s_p} \tag{5.25}$$

Equations 5.4 and 5.9 follow from Equations 5.18 and 5.19:

$$V_{saym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}}$$

and

$$V_{other,ym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \frac{\nu_{other}^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}}$$

Strictly speaking, $\tilde{\nu}_s^{s_p}$ should be a function of predator age, but since it is not feasible to estimate this parameter for all ages, an age-independent $\tilde{\nu}_s^{s_p}$ is estimated instead.

At pre-exploitation equilibrium, Equation 5.4 simplifies to

$$V_{say_0,m=1}^{s_p a_p} = \breve{N}_{y_0,m=1}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \tilde{\nu}_s^{s_p} + \tilde{\nu} O_{other}^{s_p a_p}} \tag{5.26}$$

Further, $V_{say_0,m=1}^{s_p a_p,max} = \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1+\tilde{\nu}_s^{s_p} + \tilde{\nu} O_{other}^{s_p a_p}}$, which is now independent of the (unknown) initial population size.

5.4 Likelihood components

This section describes the additions that have been made to the (penalised) negative log-likelihood described in Chapter 4 in order to be able to estimate the predation model parameters. The 1999-2013 DAFF biological data set provides good information on two aspects of the hake diet: the proportion of hake in the diet of hake predators, and the preference that a hake predator of a given age exhibits for hake prey of different ages. The equations for how this information is incorporated into the likelihood are provided in this section. A further quantity of particular relevance to the predation model is the daily ration of hake. Since no direct estimates of this quantity are available for hake, daily ration has been handled in a slightly different manner, as explained in the model development section (see Section 5.5.1).

Note that since there are no diet data available for hake predators of age $a_p = 0$ (and the model assumes that hake aged zero do not prey on hake), this age group is not included in any of the likelihood contributions from the diet data. The minimum predator length considered in the model is 19cm, which corresponds roughly to one year old hake (1.1 years for *M. capensis* and 0.93 years for *M. paradoxus*).

5.4.1 Proportion of hake in diet

The calculation of the observed proportion of hake in the diet of hake predators from the stomach content data is described in Appendix 5.B. The model-predicted proportion of hake of species s in the diet of predators of

species s_p and length class[6] L_p in year y is taken to be the total mass of hake of species s consumed by these predators in year y, divided by the total mass of all prey consumed:

$$\hat{\rho}_{sy}^{s_p L_p} = \left(\sum_m \sum_{a_p \neq 0} \left(\sum_{l_p \in L_p} A^{s_p l_p a_p} \right) Q_{sym}^{s_p a_p} \right) / \left(\sum_m \sum_{a_p \neq 0} \left(\sum_{l_p \in L_p} A^{s_p l_p a_p} \right) \left(\sum_s Q_{sym}^{s_p a_p} + Q_{other,ym}^{s_p a_p} \right) \right) \quad (5.27)$$

where $Q_{sym}^{s_p a_p}$ is the mass of hake of species s consumed by predators of species s_p and age a_p (Equation 5.6), $Q_{other,ym}^{s_p a_p}$ is the mass of other prey consumed by predators of species s_p and age a_p (Equation 5.10) and $A^{s_p l_p a_p}$ is the proportion of fish of species s_p and age a_p that are of length l_p (Section 4.2.5). $\sum_{l_p \in L_p} A^{s_p l_p a_p}$ is the proportion of fish of species s_p and age a_p that fall into the 10cm length class L_p.

The contribution to the negative log-likelihood is given by:

$$-lnL+ = -\sum_y \sum_{s_p} \sum_{L_p} \sum_s \left(\rho_{s,obs}^{s_p L_p} - \hat{\rho}_y^{s_p L_p} \right)^2 / \left(2 \left(\sigma_{\rho,s}^{s_p, L_p} \right)^2 \right) \quad (5.28)$$

where $\rho_{s,obs}^{s_p L_p}$ is the observed (year-averaged) proportion of hake in the diet of hake predators, adjusted to reflect prey mass at ingestion time and corrected for differential evacuation rates of different prey types (see Table 5.B.5 of Appendix 5.B), and $\sigma_{\rho,s}^{s_p, L_p}$ its associated standard error (see Table 5.B.6 of Appendix 5.B).

5.4.2 Preference data

The 1999-2013 DAFF biological dataset provides counts of hake prey of species s and length l in the stomachs of predators of species s_p and length l_p. The corresponding ages were calculated from the observed lengths using the pertinent von Bertalanffy growth curve[7] to obtain the counts by predator and prey ages (i.e. a form of cohort-splicing). These are provided in Table 3.9 of Chapter 3. Let these counts be denoted by $\zeta_{s,a,obs}^{s_p a_p}$, and let $\hat{\chi}_{s,a}^{s_p a_p}$ denote the model-predicted proportion of hake prey of species s and age a consumed by predators of species s_p and age a_p in year y, given by:

$$\hat{\chi}_{say}^{s_p a_p} = \frac{\sum_m E_{saym}^{s_p a_p}}{\sum_a \sum_m E_{saym}^{s_p a_p}} \quad (5.29)$$

where $E_{saym}^{s_p a_p}$ is the number of hake prey of species s and age a consumed in month m of year y by predators of species s_p and age a_p (Equation 5.5). The negative log-likelihood contribution is:

$$-lnL+ = -\sum_y \sum_{s_p, a_p \neq 0} \sum_{s,a} \zeta_{s,a,obs}^{s_p, a_p} \left(ln(\hat{\chi}_{say}^{s_p a_p}) - ln(\zeta_{s,a,obs}^{s_p a_p} / \sum_l \zeta_{s,a,obs}^{s_p a_p}) \right)$$

There is some discussion in Chapter 7 on the possibility of modeling preference directly as a function of length rather than of age.

[6] The length classes are $L_p \in \{\leq 20\text{cm};\ 21-30\text{cm};\ 31-40\text{cm};\ \ldots;\ 61-70\text{cm};\ >70\text{cm}\}$, as defined in Appendix 5.B. While data are available at 1 cm length intervals, this grouping was chosen to ensure reasonable sample sizes for each length class (see Section 5.B.3).

[7] The sex-averaged growth curves (Table 4.2) were used to calculate the ages from the recorded lengths. Strictly speaking it would be better to use the sex-specific growth curves for the stomach samples where the gender of the predator has been recorded, but given the natural variance in length in a given age class, ignoring the gender in the age-length conversion seems unlikely to introduce any major bias.

5.5 Further model development

The methods and equations presented thus far constitute what could be considered the rudimentary foundation of the predation model. This section describes the further model developments that were found necessary in order to find a reasonable fit to the data.

5.5.1 Daily ration

The model was originally fit without any constraints on daily ration, to see if it was able to produce biologically realistic estimates for this quantity. It was, however, unable to do this and produced very low levels for the *M. paradoxus* daily ration (full results are provided in Chapter 6). Hence a penalty was added to the negative-log likelihood to prevent estimates of daily ration that are outside biologically realistic bounds. The full details of how estimates of these bounds were obtained are provided in Appendix 5.C, but to summarise a lower bound of 0.1% of body mass and an upper bound of 4% of body mass were taken to be the limits of biological realism. The details of the model-predicted daily ration and likelihood contributions are provided below.

Let $\hat{\delta}_{ym}^{s_p a_p}$ be the model estimate of the total daily ration of a predator of species s_p and age a_p in month m of year y, expressed as a percentage of predator body mass, defined by:

$$\hat{\delta}_{ym}^{s_p a_p} = \frac{\sum_s Q_{sym}^{s_p a_p} + Q_{other,ym}^{s_p a_p}}{\sum_{\tilde{a}_p=12a_p}^{12a_p+11} \tilde{N}_{y,m}^{s_p,\tilde{a}_p} w^{s_p \tilde{a}_p}} \left(\frac{12}{365}\right) (100) \tag{5.30}$$

The average daily ration as a percentage of body weight, $\bar{\delta}^{s_p a_p}$, is given by:

$$\bar{\delta}^{s_p a_p} = \frac{1}{12 n_{diet}} \sum_{y_{diet}} \sum_{m=1}^{12} \hat{\delta}_{ym}^{s_p a_p} \tag{5.31}$$

where n_{diet} is the number of years (y_{diet}) for which diet data are available to the model, namely 1999-2013.

The penalty added to the negative log-likelihood is of the following form:

$$-lnL+ = \sum_{s_p,a_p \neq 0} \begin{cases} \left(\bar{\delta}^{s_p a_p} - 0.1\right)^2 / (2(0.01)^2) & \text{if } \bar{\delta}^{s_p a_p} < 0.1 \\ \left(\bar{\delta}^{s_p a_p} - 4.0\right)^2 / (2(0.1)^2) & \text{if } \bar{\delta}^{s_p a_p} > 4.0 \\ 0 & \text{otherwise} \end{cases} \tag{5.32}$$

The different values for the standard error in the numerator of each of the above equations were chosen so that the likelihood receives a much higher penalty when the daily ration drops below 0.1 by a small amount than it would when it goes above 4.0 by that same amount.

5.5.2 *M. capensis* preference for *M. capensis* compared *M. paradoxus* prey

Appendix 5.D shows that as a *M. capensis* predator grows larger and moves into deeper water, it will be more likely to encounter *M. paradoxus* than *M. capensis* prey of a preferred size. Having no depth structure, the predation model has no direct way of taking account of this shift. A depth-availability vector, $D_s^{s_p a_p}$, was

thus introduced to allow the *M. capensis* preference for *M. capensis* prey to decrease with predator age, and correspondingly increase with predator age for *M. paradoxus* prey. Equation 5.4 is consequently modified to:

$$V_{saym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} D_s^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{5.33}$$

and $\Phi_{sym}^{s_p a_p}$ from Equation 5.21 is redefined as:

$$\Phi_{sym}^{s_p a_p} = \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p} D_s^{s_p a_p}}{\sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p} D_s^{s_p a_p}} \tag{5.34}$$

The depth-availability vector is defined as

$$D_s^{s_p a_p} = \begin{cases} e^{-s_D(a_p)} & \text{for } \textit{M. capensis} \text{ predators and } \textit{M. capensis} \text{ prey} \\ e^{-s_D(a_m)} e^{s_D(a_p)} & \text{for } \textit{M. capensis} \text{ predators and } \textit{M. paradoxus} \text{ prey} \\ 1 & \text{for } \textit{M. paradoxus} \text{ predators} \end{cases} \tag{5.35}$$

where a_p is the predator age, s_D is an estimable parameter and $a_m = 15$ is the maximum age considered in the model.

5.5.3 Daily ration with predator age

At this stage of the development, the predation model still had very little informative data to estimate daily ration. The upper and lower bounds on daily ration introduced above provide no guidelines regarding what the daily ration should be between these bounds. However, the equations of Essington *et al.* (2001), which were used to obtain the upper and lower bounds for the daily ration, also provide a further guideline that a regression of the log of daily ration against the log of the body weight should yield a slope of -1/3 (see Section 5.C.4 of Appendix 5.C). This relationship was incorporated into the negative log-likelihood to provide additional information for estimating the dependence of the daily rations on predator age. If δ_{slope}^{sp} is the slope of the regression of the log of the model-estimated daily ration ($ln\bar{\delta}^{s_p a_p}$) against the log of the expected weight ($lnw^{s_p a_p}$) for a predator of species s_p, then the following penalty is added to the negative log-likelihood:

$$-lnL+ = \sum_{s_p} \left(\delta_{slope}^{sp} - \left(-\frac{1}{3} \right) \right)^2 / \left(2(\sigma_{slope})^2 \right) \tag{5.36}$$

A value of $\sigma_{slope} = 0.04$ was found to be sufficiently small to stabilise the estimation without giving undue weight to this penalty.

5.5.4 Limiting the predation mortality rate: Introducing competition

Punt (1994) introduced a competition term into his hake predation model to prevent excessive predation when large predator cohorts moved through the model, thus damping the large predator-prey oscillations exhibited by his biomass trajectories and stabilising the estimation process. Similar issues with instability were experienced in the predation model presented in this thesis when high mortality rates led to unrealistic population oscillations once the *M. paradoxus* daily ration became large enough (this is discussed further in Chapter 6). A competition effect has thus similarly been introduced to this predation model, which has been implemented using the

relatively simple approach of constraining the predation mortality rate, P_{saym}, to be less than a set limit P_{lim} through the use of an ADMB posfun[8] penalty. Several values for P_{lim} were tested, with a value of 0.06 found to be the most suitable for the base case model.

5.6 Sensitivities

Greater details of the various sensitivity runs are provided in Chapter 6, since the rationales for some of these runs rely on the results of the base case model. In summary, however, sensitivity is explored to assumptions associated with the basal mortality rate, stock-recruitment relationship, daily ration (in terms of changing the lower limit as well as attempting to fix the daily ration of predators aged 3), the proportion of hake in the diet of hake predators and the *M. paradoxus* depletion level.

The estimable parameters for the predation component of the model are listed along with their bounds in Table 5.1 below.

[8]Posfun is an ADMB function which prevents the quantity referenced from becoming negative.

Table 5.1: Predation-related parameters estimated in the model fitting procedure, in addition to those of the standard Rademeyer and Butterworth (2014b) model presented in Table 4.7. The references to the equations where the parameters first appear are also listed.

	Number of parameters	**Parameters estimated**	**Bounds enforced**	**Equation**
$\nu_s^{s_p}$	3	ν_{cap}^{cap}, ν_{par}^{cap} and ν_{par}^{par}	(0; 20)	Equation 5.4, 5.9
$\nu_{other}^{s_p}$	2	$ln\nu_{other}^{cap}$ and $ln\nu_{other}^{par}$	(-40; 10)	Equation 5.9
$\tilde{\nu}_s^{s_p}$	3	$\tilde{\nu}_{cap}^{cap}$, $\tilde{\nu}_{par}^{cap}$ and $\tilde{\nu}_{par}^{par}$	(0; 100)	Equation 5.4, 5.9
$\tilde{\nu}_{other}^{s_p}$	2	$ln\tilde{\nu}_{other}^{cap}$ and $ln\tilde{\nu}_{other}^{par}$	(0; 30)	Equation 5.9
α^{s_p}	2	α^{cap}, α^{par}	(1; 150)	Equation 5.13
$\tilde{G}_s^{s_p}$	3	$\tilde{G}_{cap}^{cap}$, $\tilde{G}_{par}^{cap}$ and $\tilde{G}_{par}^{par}$	(0.1; 2)	Equation 5.13
o^{s_p}	2	o^{cap} and o^{par}	(-20; 30)	Equation 5.12
$\tilde{o}^{s_p}$	2	$ln\tilde{o}^{cap}$ and $ln\tilde{o}^{par}$	(-20; 50)	Equation 5.12
ω^{s_p}	2	ω^{cap} and ω^{par}	(0; 20)	Equation 5.15
$\tilde{\omega}^{s_p}$	2	$\tilde{\omega}^{cap}$ and $\tilde{\omega}^{par}$	(0; 20)	Equation 5.15
s_D	1	s_D	(0; 1)	Equation 5.35
Total	**24**			

Appendices

5.A Summary of the related recommendations by the panel for the International Stock Assessment workshops 2011—2015

A week-long International Stock Assessment Workshop (IWS) has been held annually since 2000 at the University of Cape Town (UCT), South Africa, co-hosted by UCT's Marine Research and Management Group (MARAM) and the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (DAFF). The purpose of the workshop is for a panel of typically three to five international experts (with partial continuity from year to year) in the field of fisheries assessment and management to review and provide advice on various key aspects of analyses related to the assessment and management of South African renewable marine resources. The workshops are attended by the scientists responsible for developing the assessment models (usually from MARAM), biologists involved in the data collection and analyses, scientists from various institutions and representatives from DAFF, as well as representatives from the fishing industries. The panel and participants at the workshops provide valuable insights into current issues and the panel provides advice for future developments of assessments in their report.

The hake predation model was presented for the first time at IWS 2011, and again in 2013, 2014 and 2015. Many of the major model developments and improvements arose from recommendations made at these workshops. Table 5.A.1 provides a summary of the recommendations that have been made over the years, along with the status of their implementation and a priority assignment (by the author of this thesis) for those recommendations that have not been implemented.

Table 5.A.1: Recommendations pertinent to the hake predation model made by the panels for the 2011 (Smith *et al.* 2011), 2013 (Smith *et al.* 2013), 2014 (Dunn *et al.* 2014) and 2015 (Dunn *et al.* 2015) International Stock Assessment workshops. The recommendations have been sorted by category, and a current status for each has been provided. A '-' indicates that the recommendation in question has been implemented. For recommendations that have not yet been implemented, the author's priorities have been allocated as high (H), medium (M) or low (L). Note however that a priority marked with an asterisk indicates that this priority was allocated directly by the workshop panel.

(A) Spatial structure			
Recommendation	**Date**	**Current status**	**Priority**
A1. Start with South Africa only, and perhaps incorporate Namibian data later if possible.	IWS 2011	The model considers South Africa only. Incorporation of Namibian data seems unlikely to occur in the near future.	L
A2. Exclude South Coast initially, but implement coastal segregation later if possible since feeding will likely differ on the two coasts.	IWS 2011	The current model has no coastal segregation, and the model uses diet data from the West Coast only.	H*

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Table 5.A.1: *...continued from the previous page*

A3. Explicitly account for spatial structure, either using a movement model or by treating predation on the West and South coasts as separate 'fleets' (base initial analyses on diet data for the West Coast only).	IWS 2014	Coastal segregation is a high priority.	H*
A4. No depth segregation.	IWS 2011	The model does not have depth segregation, and such segregation may be difficult to implement given the already complex nature of the predation model. Depth segregation has, however, been taken into account to some extent in the current predation model, by allowing the *M. capensis* preference for *M. capensis* and *M. paradoxus* prey to change with depth (see Section 5.5.2 and recommendation E11).	L
(B) Population structure			
Recommendation	**Date**	**Current status**	**Priority**
B1. Ignore sex structure initially. Only later extend model to something similar to the current hake assessment model.	IWS 2011	The model is sex-aggregated in its current form.	-
B2. Disaggregate the model by sex to better fit, for example, the longline catch-at-age data. It should be possible to disaggregate the diet data by predator sex but not by prey sex.	IWS 2014	Sex-disaggregation should be implemented.	H*
B3. Do not fit to catch-at-length (CAL) and age-length-key (ALK) data initially.	IWS 2011	The model does not fit to CAL or ALK data, but this could be considered in the future.	M/L
B4. Implications of whether recruitment is taken to occur before or after predation should be explored.	IWS 2013	This has not been explored yet, but has been noted for possible future work.	M/H
B5. Consider alternate formulations of stock-recruit models for hake that incorporate cannibalism, both directly as a covariate and indirectly in how spawning stock biomass is defined (e.g. Link *et al.* 2012).	IWS 2014	This may be investigated in the future, time permitting.	L

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Table 5.A.1: *...continued from the previous page*

(C) Diet data			
Recommendation	**Date**	**Current status**	**Priority**
C1. Scale hake prey-by-species information upwards to account for unidentified hake prey.	IWS 2013	This applies to *M. capensis* predators, since *M. paradoxus* are assumed to consume *M. paradoxus* only. Further investigation is required.	M
C2. Difference in feeding relationship between West and South Coast should be investigated.	IWS 2013	This has not yet been undertaken, but should be investigated in conjunction with recommendations A2 and A3.	H
C3. The proportion of hake in the diet of hake predators should be based on estimated mass-at-ingestions, rather than on counts of prey items.	IWS 2015	This recommendation has been implemented, as described in Appendix 5.B.	-
C4. Plan, and then implement, a review of the sampling strategy for diet data given the results of the current model as well as other needs for diet data.	IWS 2014	This recommendation pertains to DAFF, and has been noted here for the record.	H*
C5. The diet data should be developed based on predator age rather than predator length, since most hake for which stomach content data are analysed are aged. The use of such data in the predation model would simplify the fitting process since the model is age-based.	IWS 2015	This has been noted by DAFF.	M*
(D) Other predators			
Recommendation	**Date**	**Current status**	**Priority**
D1. Do not include other predators (seals) initially, but if there is an increase/decrease in seal population try take this into account in the mortality rates.	IWS 2011	The model currently does not include specific predators other than hake, but the possibility of including seal predators will be explored in the future.	H
D2. Include other predators (re-evaluate sources of hake mortality to identify which predators to add to the model).	IWS 2014	The inclusion of other predators (in particular seals and large predatory fish) will be explored in the future.	H

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Table 5.A.1: *...continued from the previous page*

(E) Technical modelling aspects of the predation and cannibalism model			
Recommendation	**Date**	**Current status**	**Priority**
E1. Test different values for basal mortality, particularly lower values.	IWS 2014	This has been considered in this thesis.	-
E2. A Holling Type II functional form should be implemented initially, but other forms (as in Kinzey and Punt 2009) could be explored, including Holling Type III or Foraging Arena.	IWS 2011	The model uses a Holling Type II functional form. Other forms should be explored in the future.	M
E3. Use the hybrid method with a Baranov formulation for catch equation.	IWS 2013	This has been implemented.	-
E4. Daily ration should not be prespecified but rather included as a likelihood component.	IWS 2013	This has been implemented, and daily ration is no longer a fixed quantity in the model.	-
E5. The feeding functional response should be parameterised to simplify the equilibrium setup.	IWS 2013	This has been implemented.	-
E6. Include an "other food" component as in Kinzey and Punt (2009).	IWS 2013	This has been implemented.	-
E7. Apply the model ignoring the spatial availability matrix (Appendix A of MARAM/IWS/DEC14/Hake/P8) to assess whether this feature of the model is needed to allow the model to mimic the observed diet compositions by age.	IWS 2014	This has been implemented. The model seems to cope without the spatial availability matrix, so that this feature has been discontinued.	-
E10. The preference function should be normalised to sum to one across all hake prey species and ages.	IWS 2015	This has been implemented.	-
E11. Allowance should be made for predation to differ between prey species and ages in the predation function.	IWS 2015	This has been implemented (see for example the depth availability vector in Section 5.5.2).	-
E12. The plus-group should be extended from 10+ to 15+.	IWS 2015	This has been implemented.	-

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Table 5.A.1: *...continued from the previous page*

(F) Data conflicts			
F1. When conflict is experienced between the model fitting to the historical ICSEAF CPUE trend *versus* the diet data, priority should be given to the fit to the CPUE data since major reductions in catch rates are an important characteristic of southern African hake fisheries between the early- to mid-1960s and mid-1970s.	IWS 2015	This priority has been respected in the results presented in this thesis.	-
F2. Likelihood components for the proportions of hake prey in the diets of hake predators of various lengths should be weighted appropriately if there is evidence of overdispersion.	IWS 2015	Following the revised calculations for the proportion of hake in the diet of hake (Appendix 5.B), the likelihood contributions for these proportions have become much more comparable with other likelihood components in the model. This should, however, be considered further in the future.	M*

5.B Estimating the proportion of hake in the diet of hake predators

Diet data provide a break-down of stomach content information for each predator species (s_p), predator length class (l_p), year (y) and depth stratum (d). In order to obtain an estimate of the proportion of hake prey in the diet of hake predators, the prey items are classified as hake prey and 'other' prey, with 'other' prey further disaggregated into 'fish', 'crustacean' and 'mollusc' (mainly cephalopods) groups which allows for the use of varying evacuation rates for different prey types.

The proportion of hake in the diet of hake predators is calculated following the recommendations of the panel of IWS 2015 (Dunn *et al.* 2015). The proportions of *M. capensis* and *M. paradoxus* prey are calculated separately for *M. capensis* predators; because of an absence of spatial overlap, *M. paradoxus* predators have no *M. capensis* prey. The proportion for each hake predator and prey species pairing is as follows:

$$\rho_{s,y,d}^{s_p,l_p} = \frac{\Omega_{s,y,d}^{s_p,l_p}/T_s}{\sum_{s'} \Omega_{s',y,d}^{s_p,l_p}/T_{s'}} \tag{5.B.1}$$

where

- $\rho_{s,y,d}^{s_p,l_p}$ is the proportion of hake of species s in the stomachs of hake predators of species s_p and length l_p, calculated from samples collected in year y and depth stratum d,
- $\Omega_{s,y,d}^{s_p,l_p}$ is the total estimated mass (at ingestion) of prey of species s consumed by hake predators of species s_p and length l_p in samples collected in year y and depth stratum d, and
- T_s is the time taken to evacuate a prey item of species s.

Note that the summation $\sum_{s'}$ extends over both hake and other prey species.

5.B.1 Obtaining an estimate of mass-at-ingestion

In order to obtain the $\Omega_{s,y,d}^{s_p,l_p}$ values, the observed mass for each prey item in the stomachs of hake predators has to be converted to a mass at ingestion. The panel for the 2015 International Stock Assessment Workshop recommended that an approach be taken similar to that taken by Punt and Leslie (1995) for Cape hake predators, with a few modifications (Dunn *et al.* 2015).

5.B.1.1 The Punt and Leslie (1995) approach for obtaining mass-at-ingestion

The Punt and Leslie (1995) approach is outlined below.

1. If the number of items and their lengths are recorded, and if the length-mass relationship is available for the prey species concerned, then the length-mass relationship is used to estimate ingested mass based on observed length. If the estimate of ingested mass obtained by means of this approach is smaller than the actual mass of the stomach contents, the latter is used instead as an estimate of ingested mass. This problem can occur when a prey item is in digestion stages 1 (very fresh) or 2 (partially digested).
2. If the prey item is a crustacean or a cephalopod, then the ingested mass is estimated by multiplying the observed stomach contents by 2. This is equivalent to assuming that, on average, the stomach contents reflect material half-way through the digestion cycle and that digestion is a linear process.

3. If the prey item is a fish, but either the length-mass relationship has yet to be determined for the species concerned, or the number of prey items or the length was not recorded, then the following equation is solved for ingested mass (note that the temperature T is assumed to be 9°C)[9]:

$$S_t^{1-\beta} = S_0^{1-\beta} - \alpha_1 e^{\alpha_2 9} (1-\beta) (BW/600)^{\alpha_3} (S_0/BW)^{\alpha_4} (T_{90}/2) \quad (5.B.2)$$

where

T_{90}	is the time to evacuate 90% of a fish prey item for the hake predators in the length class concerned (Table 5.B.3),
BW	is the body mass of the hake predator, calculated from the recorded predator length,
S_t	is the observed mass of the prey item in the stomach,
S_0	is the mass at ingestion, and
$\beta, \alpha_1, \alpha_2, \alpha_3, \alpha_4$	are parameters (see Table 5.B.2).

5.B.1.2 Taking digestion state into account

Step 2 of Punt and Leslie (1995) is refined further to take the recorded digestion state (DS) into account (R.W. Leslie, *pers. comm.*, Dunn *et al.* 2015). Five levels of DS are recorded in the dataset:

0. No signs of digestion or of damage that would be expected if the prey item had been captured by the predator. Since these prey items were probably ingested during the trawl, these samples have been removed from this analysis.
1. Very fresh with no or only slight signs of digestion. If there are no signs of digestion, this state differs from '0' in that there are signs of injuries received during capture by predator.
2. Partially digested.
3. Well digested.
4. So well digested that the prey items are unrecognisable. Note that samples where prey species were labelled as 'unidentified matter' were excluded from this analysis.

The following multiplicative factors have been applied for the different digestive states as the base case assumption:

DS=0	-	Exclude.
DS=1	-	Use observed mass.
DS=2 or 3	-	Multiply by 2.
DS=4	-	Multiply by a number larger than 2; either 3 or 4 as detailed in Table 5.B.4.

5.B.1.3 Accounting for several prey fish of the same species

There are samples in the database for which several prey items of the same species were found in the stomach of a single predator, in which case a combined mass was recorded for all the prey items of that species. Where such samples correspond to fish prey, individual masses and lengths have been interpolated for each prey item.

[9] Punt and Leslie (1995) tested whether this assumption is reasonable by investigating the difference between the mass-at-ingestion estimated for prey items for which the length-mass relationship is available using method 1 as well as method 3. They found only a 10% difference between the two methods.

Prey fish for which a mass-length relationship and prey length are available

Given a stomach sample with n prey fish of the same species, let w_i^{WL} be the mass-at-ingestion of prey item i calculated from the mass-length relationship, and let w_i^{rec} be the 'recorded' (i.e. partially digested) mass of prey item i derived from the total recorded mass. If minimum (l_{min}) and maximum (l_{max}) prey lengths were recorded, n lengths are calculated by linear interpolation between l_{min} and l_{max}. These lengths are then used to calculate mass-at-ingestion (w_i^{WL}) using the mass-length relationship. The breakdown of the recorded weight for each prey item i (w_i^{rec}) is calculated under the assumption that (a) $w_i^{rec} \propto al_i^b$, where a and b are given by the mass-length relationship, and (b) $w_i^{rec}/w_j^{rec} = (l_i/l_j)^b$for all prey items i and j in the stomach. If W^{rec} is the combined mass recorded for the n prey items, then $\sum_i w_i^{rec} = W^{rec}$. From the above it follows that $w_i^{rec} = W^{rec}/\left(1 + \sum_{j\neq i}(l_j/l_i)^b\right)$ for $i \in (1, n)$. If the mass calculated from the mass-length relationship (w_i^{WL}) is less than the mass derived from the recorded mass (w_i^{rec}), then the latter is used as the estimate of mass-at-ingestion.

Prey fish for which a mass-length relationship and/or prey length are not available

If the mass-length relationship is not available, or the prey lengths have not been recorded, then the mass-in-stomach for each item is assumed to be simply W/n, where W is the combined mass recorded for the n prey items. The mass W/n is then used for S_t in Equation 5.B.2 to estimate a mass at ingestion.

Other (non-fish) prey items

Since the recorded mass of a prey item that is not fish is simply scaled upwards according to digestion state, there is no need to separate out several prey items of the same species in these cases, as they have all been allocated the same digestion state in the database.

5.B.2 Time to evacuate, T_S

The arguments presented below have already been made earlier in this thesis, but have been included here for the reader's ease and in the interest of completeness.

No evacuation experiments are known to have been performed on hake, so that no estimates of the time taken to evacuate a hake predator's stomach are available. Notable work on Cape hake (Prénski 1980, Payne *et al.* 1987, Punt *et al.* 1992, Punt and Leslie 1995) base estimates of evacuation time on data provided in Jones (1974) for haddock (*Melanogrammus aeglefinus*), cod (*Gadus morhua*) and whiting predators (*Merlangius merlangus*).

Table 1 of Prénski 1980 provides a range of evacuation rates (in hours) for fish prey and crustacean prey. The average of these values has been used as an estimate of evacuation time for fish prey (75 hours, or 3.13 days) and crustacean prey (32 hours or 1.33 days) for Equation 5.B.1. Payne *et al.* (1987), Punt *et al.* (1992) and Punt and Leslie (1995) argue that cephalopods would take longer than crustacean but shorter than fish prey to digest, with an evacuation time closer to the former, and implement a value 50% greater than the value for assumed for crustaceans[10]. Following this argument, an intermediate value of 48 hours (2.00 days) has been used for cephalopod prey.

[10]Payne *et al.* (1987), Punt *et al.* (1992) and Punt and Leslie (1995) assume evacuation times of 3 days for fish, 1 day for crustaceans and 1.5 days for cephalopods.

5.B.3 Stratum-aggregated proportion

The stratum-aggregated proportion of hake in the diet of hake predators is calculated from the stratum-disaggregated proportion (Equation 5.B.1) as follows:

$$\rho_{s,y}^{s_p,l_p} = \frac{\sum_d \rho_{s,y,d}^{s_p,l_p} N_{y,d}^{s_p,l_p}}{\sum_d N_{y,d}^{s_p,l_p}} \tag{5.B.3}$$

where

$\rho_{s,y}^{s_p,l_p}$ is the stratum-aggregated proportion of hake of species s found in the stomachs of hake predators of species s_p and length l_p in year y,
$\rho_{s,y,d}^{s_p,l_p}$ is the corresponding stratum-disaggregated proportion from Equation 5.B.1, and
$N_{y,d}^{s_p,l_p}$ is the survey estimate of population abundance (in numbers) of hake of species s_p and length l_p in depth stratum d in year y.

However, given the substantial number of samples containing empty or everted stomachs (see Tables 3.6a and 3.6b), the exclusion of these samples leaves a relatively sparse data set, in particular for larger *M. paradoxus* predators. Thus Equation 5.B.3 has been adjsuted so that the data are binned into 10cm predator length classes, leading to an equation:

$$\rho_{s,y}^{s_p,L_p} = \frac{\sum_d \rho_{s,y,d}^{s_p,L_p} \left(\sum_{l_p \in L_p} n_{y,d}^{s_p,l_p} N_{y,d}^{s_p,l_p} \right)}{\sum_d \sum_{l_p \in L_p} n_{y,d}^{s_p,l_p} N_{y,d}^{s_p,l_p}} \tag{5.B.4}$$

where

$$\rho_{s,y,d}^{s_p,L_p} = \frac{\sum_{l_p \in L_p} \Omega_{s,y,d}^{s_p,l_p} / T_s}{\sum_{s'} \sum_{l_p \in L_p} \Omega_{s',y,d}^{s_p,l_p} / T_{s'}} \tag{5.B.5}$$

The length classes are defined as $L_p \in \{\leq 20\text{cm};\ 21-30\text{cm};\ 31-40\text{cm};\ \ldots;\ 61-70\text{cm};\ >70\text{cm}\}$.

Even given this binning, the annual sample sizes for some strata, particularly for the larger predators at larger depths, are in the single figures. This means that although the estimates provided by Equation 5.B.4 are unbiased, some components of the right hand side will have relatively high variance. This is, to some extent, taken into account through the variance estimation procedure set out in Section 5.B.5 below.

5.B.4 Year-aggregated proportion

The stratum-aggregated proportions vary substantially across the years, especially for the larger length groups (Figures 5.B.1 and 5.B.2). This may in part be due to the relatively small numbers of non-empty and non-everted stomach samples available for these larger length groups. Accordingly, a sample-size weighted mean is calculated for each length group across all years:

$$\rho_{s,obs}^{s_p,L_p} = \frac{\sum_y n_y^{s_p,L_p} \rho_{s,y}^{s_p,L_p}}{\sum_y n_y^{s_p,L_p}} \tag{5.B.6}$$

where

$\rho_{s,obs}^{s_p,L_p}$ is the year-aggregated proportion of hake of species s in the diet of hake predators of species s_p and length group L_p,

$n_y^{s_p,L_p}$ is the number of non-empty stomachs of hake predators of species s_p and length group L_p that were sampled in year y, and

$\rho_{s,y}^{s_p,L_p}$ is the year-disaggregated proportion of hake in the hake diet as defined in Equation 5.B.4.

The proportions of hake in the diet as defined in Equation 5.B.6 are used to inform the negative log-likelihood of the hake predation model.

5.B.5 Estimate of the variance of the proportion of hake in the diet

In the model fitting process, the model values for the proportions of hake in the diet for predator species s_p and length lp changes from year to year. Hence, although the data have had to be aggregated over years to obtain reasonably stable values, the variance used to inverse-weight each annual comparison of data– and model-based proportions in the negative log-likelihood (see Section 5.4.1 of Chapter 5) needs to reflect not only the uncertainty in the mean estimate from the data over all the years, but also the extent to which these data suggest that these values vary from year to year. This has accordingly been calculated as follows:

$$\left(\sigma_{\rho,s}^{s_p,L_p}\right)^2 = \left(\sigma_{\mu,s}^{s_p,L_p}\right)^2 + \left(\sqrt{N}\sigma_{Y,s}^{s_p,L_p}\right)^2 \tag{5.B.7}$$

where

$\left(\sigma_{\rho,s}^{s_p,L_p}\right)^2$ is the overall variance of the proportion of hake in the diet estimate $\rho_{s,obs}^{s_p,L_p}$, -

$\left(\sigma_{\mu,s}^{s_p,L_p}\right)^2$ is the variance of the mean of $\rho_{s,obs}^{s_p,L_p}$,

$\left(\sigma_{Y,s}^{s_p,L_p}\right)^2$ relates to the extent of inter-annual variation, and

$N = \sum_y 1$ is the number of years for which diet data are available, in this case 14 years between 1999 and 2013.

The variance of the mean, $\left(\sigma_{\mu,s}^{s_p,L_p}\right)^2$, is estimated using the jackknife approach:

$$\left(\sigma_{\mu,s}^{s_p,L_p}\right)^2 = \frac{N-1}{N}\sum_{i=1}^{N}\left(\rho_{s,JN(i)}^{s_p,L_p} - \rho_{s,obs}^{s_p,L_p}\right)^2 \tag{5.B.8}$$

where $\rho_{s,obs}^{s_p,L_p}$ is the proportion of hake in diet as defined in Equation 5.B.6 and $\rho_{s,JN(i)}^{s_p,L_p}$ is the jackknife estimate obtained by omitting the i^{th} year in Equation 5.B.6, i.e.:

$$\rho_{s,JN(i)}^{s_p,L_p} = \frac{\sum_{y\neq y_i} n_y^{s_p,L_p}\rho_{s,y}^{s_p,L_p}}{\sum_{y\neq y_i} n_y^{s_p,L_p}} \tag{5.B.9}$$

The contribution of the inter-annual variability to the overall variance of the mean is calculated as follows:

$$\left(\sigma_{Y,s}^{s_p,L_p}\right)^2 = \left(\sigma_{\mu,s}^{s_p,L_p}\right)^2 - \left(\sigma_{S,s}^{s_p,L_p}\right)^2 \tag{5.B.10}$$

where $\left(\sigma_{S,s}^{s_p,L_p}\right)^2$ is the sampling variance arising from the limited numbers of samples available to estimate the mean, which is estimated by assuming that a binomial distribution underlies the proportion of hake in diet:

$$\left(\sigma_{S,s}^{s_p,L_p}\right)^2 = \frac{\rho_{s,obs}^{s_p,L_p}\left(1-\rho_{s,obs}^{s_p,L_p}\right)}{\sum_y n_y^{s_p,L_p}} \tag{5.B.11}$$

Thus the contribution to the variance of the mean arising from true inter-annual variation is assumed to be provided by the difference between jackknife and binomial estimate of the overall variance, since the latter ignores the effect of inter-annual variation.

5.B.6 Excluded data points

Gastropods

There were five samples of gastropods recorded as prey items. Since most of their mass is indigestible shell, these five samples (totalling 40g) have been excluded as advised by R. Leslie (*pers. comm.*).

Unidentified prey items

All prey items marked as "unidentified matter" have been excluded when calculating the proportion of hake in the diet, as these samples do not provide further information when calculating these proportions. There is, however, only one such sample for the dataset from the West Coast. Prey items marked as "unidentified fish" (329 samples on the West Coast) are assumed not to be hake as it is unlikely that hake prey items would be unidentifiable, even at an advanced level of digestion (R. Leslie *pers. comm.*).

Prey items assumed to have been swallowed in the trawl

Prey items with a recorded digestion state of 0 (no sign of digestion or damage) are assumed to have been ingested during the trawl and have been excluded from the calculations (Punt and Leslie 1995, Payne et al. 1987)), as detailed in Section 5.B.1.2.

5.B.7 Results and conclusions

Table 5.B.4 lists the base case assumptions used to calculate the proportion of hake in diet, along with five sensitivities. The resulting proportions for the base case are provided in Table 5.B.5, while Table 5.B.6 provides the three variance components from Equation 5.B.7 for the base case. Figures 5.B.1 and 5.B.2 provides an illustration of the proportion of hake in diet for the base case and the five sensitivities. Figures 5.B.1 and 5.B.2 suggests that the year-aggregated, sample-size weighted proportion of hake in diet is not very sensitive to the range of assumptions tested here, consequently only the proportions resulting from base case assumptions are used to inform the negative log-likelihood of the predation model and the sensitivity tests reported in Chapter 6.

Figure 5.B.3 shows the sample-size weighted proportions of hake in diet for the earlier 1999-2006 period compared to the later 2007-2013 period. Except when considering the proportion of *M. capensis* prey in the diet of *M. capensis* predators, there is no obvious and large change over time, indicating that the year-aggregated approach of Equation 5.B.6 is unlikely to introduce substantial biases. In the case of *M. capensis* prey in the diet of *M. capensis* predators, since these proportions are small in both the earlier and later time periods, working with year-aggregated proportions (in contrast to year-disaggregated proportions) is unlikely to have a substantial impact on the results from the predator model.

Table 5.B.1: Available relationships between length (l) in cm and mass (w) in g for fish prey species. The relationship is given by $w = al^b$, where the units of a are g/cm^b.

Species	a	b	Source
Atractoscian aequidens	0.00862	3.0100	Mann (2013)
Austroglossus	0.00390	3.1190	Punt and Leslie (1995)
Chelidonichthys capensis	0.03470	2.6780	Punt and Leslie (1995)
Chelidonichthys queketti	0.05270	3.1200	Booth (1997)
Engraulis japonicus capensis	0.00924	3.0460	Punt and Leslie (1995)
Etrumeus whiteheadi	0.01220	2.9750	Punt and Leslie (1995)
Genypterus capensis	0.00080	3.4200	Punt and Leslie (1995)
Lophius vomerinus	0.01050	3.0204	Walmsley *et al.* (2005)
Merluccius	0.00505	3.1130	Punt and Leslie (1995)
Merluccius capensis	0.00500	3.1130	Punt and Leslie (1995)
Merluccius paradoxus	0.00620	3.0460	Punt and Leslie (1995)
Pomatomus saltatrix	0.01430	2.9800	Mann (2013)
Pterogymnus laniarius	0.02150	3.0310	Mann (2013)
Rhabdosargus globiceps	0.01660	3.0790	Mann (2013)
Sardinops sagax ocellatus	0.00957	3.0750	Punt and Leslie (1995)
Scomber japonicus	0.00155	3.4450	Punt and Leslie (1995)
Sufflogobius bibarbatus	0.01430	3.0540	Punt and Leslie (1995)
Thyrsites atun	0.00705	3.0700	Mann (2013)
Trachurus trachurus capensis	0.01240	2.9030	Punt and Leslie (1995)

Table 5.B.2: Estimates of the parameters of Equation 5.B.2 taken from Punt and Leslie (1995) for two cases: one where α_3 and α_4 are fixed at zero, and the other where they are estimated.

Length class (cm)	$\alpha_3 = 0$; $\alpha_4 = 0$	α_3, α_4 estimated
α_1	0.0248	0.0268
α_2	0.1	0.1
α_3	0	0.054
α_4	0	0.000
β	0.625	0.602

Table 5.B.3: Time taken to evacuate 90% of a hake predator's stomach (T_{90} of Equation 5.B.2). Estimates are taken from Punt and Leslie (1995) for the same two cases as in Table 5.B.2.

Length class (cm)	$\alpha_3 = 0$; $\alpha_4 = 0$	α_3, α_4 estimated
≤ 20	51.6	57.7
21-30	66.9	69.2
31-40	100.7	99.8
41-50	124.1	119.2
50-60	161.7	151.8
60-70	169.7	155.7
> 70	222.8	200.6

Table 5.B.4: Base case (BC) and sensitivity specifications for calculating the estimates of the proportion of hake in the diet of hake predators. The first column pertains to whether or not the proportions are weighted by stratum abundance (Equation 5.B.3). The second column reflects sensitivity to including or excluding samples collected in the 501-1000m depth stratum. Since samples have been collected from this stratum only in later years, survey estimates of abundance are generally not available for the stratum. In order to be able to include these samples and weight by stratum-abundance, they are essentially treated as samples from the 401-500m depth stratum. The third column pertains to the relative differences in evacuation times assumed for different prey types, while the fourth column reflects sensitivity to different multiplicative factors for the digestion state. The last column reflects sensitivity to the choice of parameters for Equation 5.B.2.

Case	Include stratum-abundance weighting	Include 501-1000m depth samples	Evacuation times Fish:Crust:Ceph	Digestion state DS_1:$DS_{2/3}$:DS_4	S_t parameters (Equation 5.B.2)
BC	Yes	Yes	75h : 32h : 48h	1 : 2 : 3	$\alpha_3 = 0$; $\alpha_4 = 0$
Sen1	**No**	Yes	75h : 32h : 48h	1 : 2 : 3	$\alpha_3 = 0$; $\alpha_4 = 0$
Sen2	Yes	**No**	75h : 32h : 48h	1 : 2 : 3	$\alpha_3 = 0$; $\alpha_4 = 0$
Sen3	Yes	Yes	**1 : 1 : 1**	1 : 2 : 3	$\alpha_3 = 0$; $\alpha_4 = 0$
Sen4	Yes	Yes	75h : 32h : 48h	**1.5 : 3 : 4**	$\alpha_3 = 0$; $\alpha_4 = 0$
Sen5	Yes	Yes	75h : 32h : 48h	1 : 2 : 3	α_3, α_4 **estimated**

Table 5.B.5: Estimated proportion of hake in the diet of hake predators, calculated using Equation 5.B.6 and the base case assumptions of Table 5.B.4.

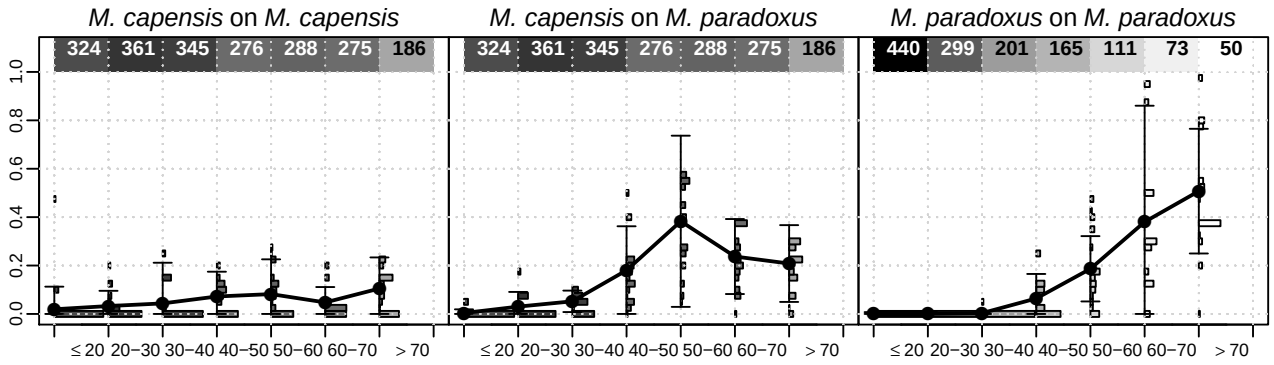
	Predator	Prey	≤20cm	20-30	30-40	40-50	50-60	60-70	≥ 70cm
$\rho_s^{s_p,L_p}$	*M. capensis*	*M. capensis*	0.02	0.03	0.04	0.07	0.08	0.05	0.10
	M. capensis	*M. paradoxus*	0.00	0.03	0.05	0.18	0.38	0.24	0.21
	M. paradoxus	*M. paradoxus*	0.00	0.00	0.00	0.06	0.19	0.38	0.51

Table 5.B.6: Estimated variances are provided for the base case proportion of hake values in Table 5.B.5. $(\sigma_{\rho,s}^{s_p,L_p})^2$ is the overall variance, while $(\sigma_{\mu,s}^{s_p,L_p})^2$ is the variance of the mean and $(\sigma_{Y,s}^{s_p,L_p})^2$ is a measure of the inter-annual variance (see Equation 5.B.7).

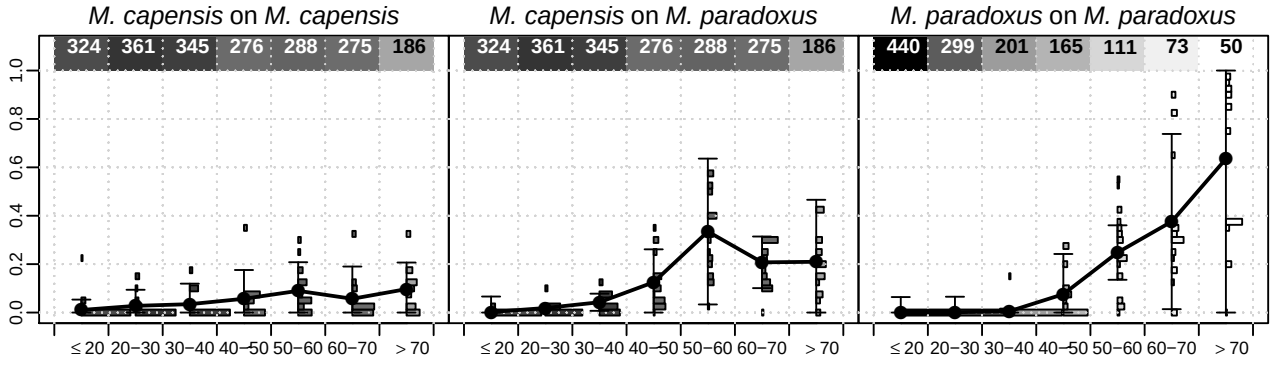
	Predator	Prey	≤20cm	20-30	30-40	40-50	50-60	60-70	≥ 70cm
$\sigma_{\rho,s}^{s_p,L_p}$	*M. capensis*	*M. capensis*	0.047	0.031	0.084	0.051	0.072	0.032	0.064
	M. capensis	*M. paradoxus*	0.032*	0.030	0.022	0.091	0.177	0.077	0.079
	M. paradoxus	*M. paradoxus*	0.032*	0.032*	0.032*	0.051	0.067	0.240	0.129
$\sigma_{\mu,s}^{s_p,L_p}$	*M. capensis*	*M. capensis*	0.014	0.012	0.024	0.020	0.024	0.015	0.027
	M. capensis	*M. paradoxus*	0.004	0.012	0.013	0.032	0.053	0.032	0.026
	M. paradoxus	*M. paradoxus*	0.000	0.001	0.002	0.023	0.040	0.083	0.076
$\sigma_{Y,s}^{s_p,L_p}$	*M. capensis*	*M. capensis*	0.012	0.008	0.022	0.013	0.018	0.008	0.016
	M. capensis	*M. paradoxus*	0.002	0.007	0.005	0.023	0.045	0.019	0.024
	M. paradoxus	*M. paradoxus*	0.000	-	-	0.012	0.015	0.060	0.028

* The sampling standard error was bigger than the standard error of the mean (possibly arising from small sample size effects), and the value of the inter-annual variation, $\sigma_{\rho,s}^{s_p,L_p}$, was fixed at what was considered a reasonable value from considerations of values estimated for adjacent length bins.

(i) Base case



(ii) Sen1 (No stratum-abundance weighting)



(iii) Sen2 (Exclude samples from 501-1000m depth stratum)

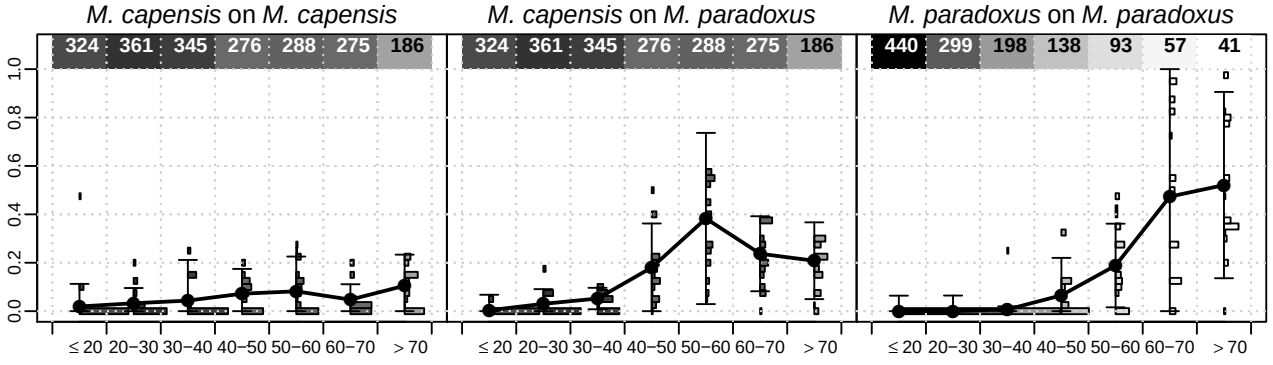
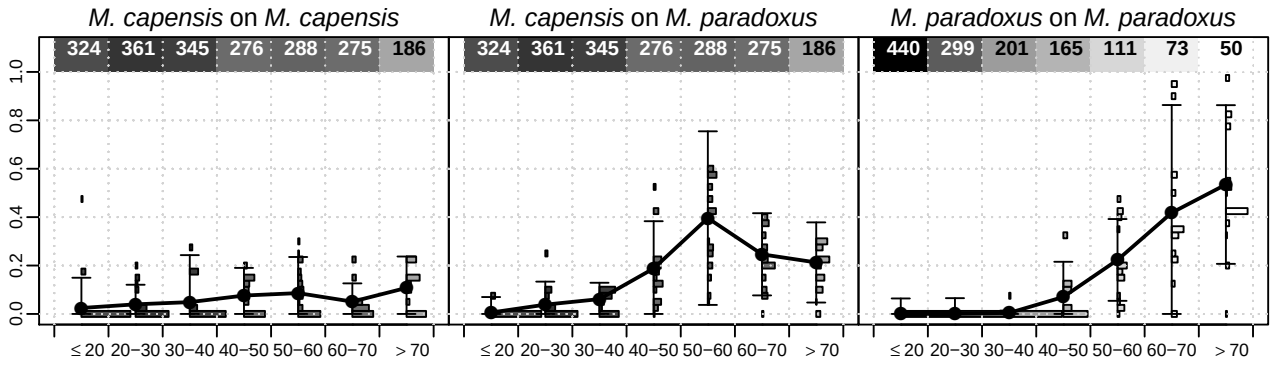
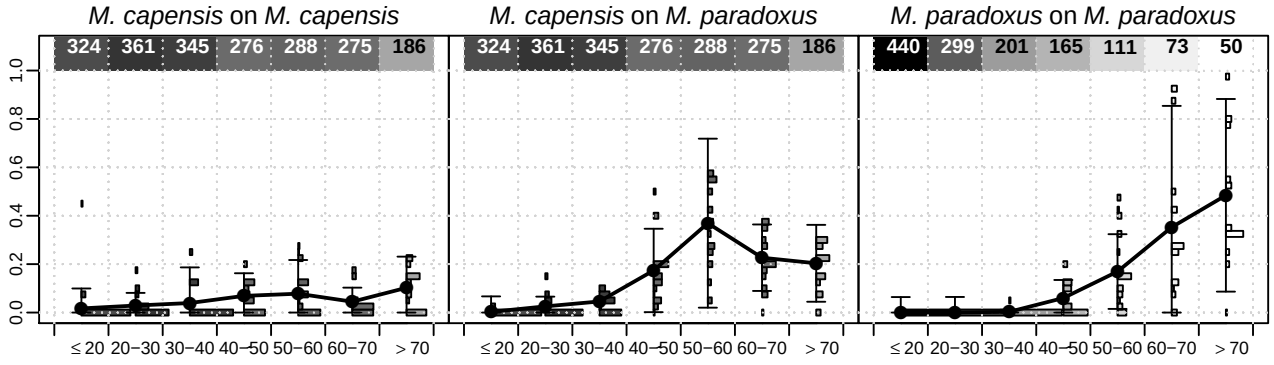


Figure 5.B.1: Estimated proportion of hake in the diet of hake predators for the base case and two of the five sensitivities (see Table 5.B.4) in terms of predator lengths shown in cm. The individual horizontal bars provide the proportions calculated on a yearly basis (Equation 5.B.4), with the size of each bar proportional to the sample size for that year relative to the total sample size across all years for the length bin in question. The sample-size weighted proportions (Equation 5.B.6) are indicated by the solid black lines, and the 95% probability interval (twice the standard error from Equation 5.B.7) by the error bars. The number in the shaded block at the top of each length group gives the total number of samples of hake predators (with non-empty and non-everted stomachs) collected for that length group over the years 1999-2013.

(i) Sen3 (Equal evacuation times for different prey types)



(ii) Sen4 (Higher multiplicative factors for digestion state)



(iii) Sen5 (Alternative values for parameters of S_t, Equation 5.B.2)

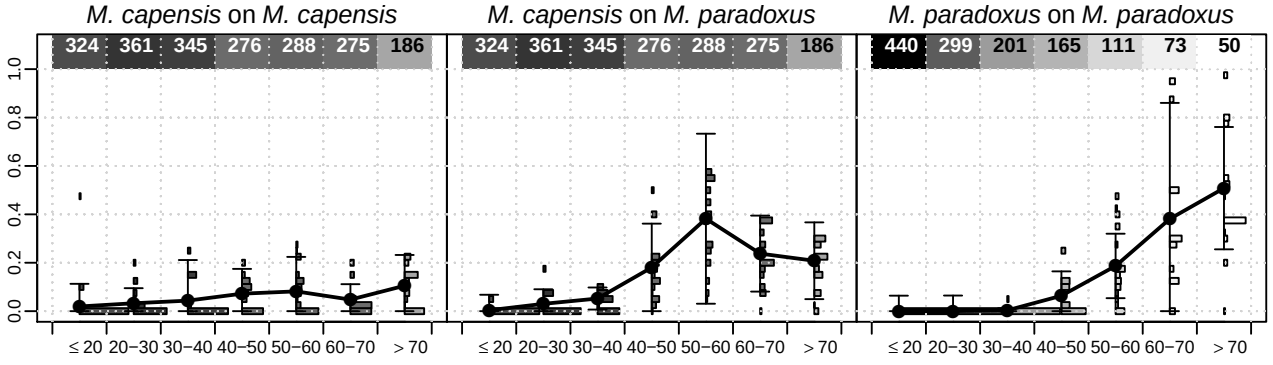


Figure 5.B.2: Continuation of Figure 5.B.1 for the remaining three sensitivities.

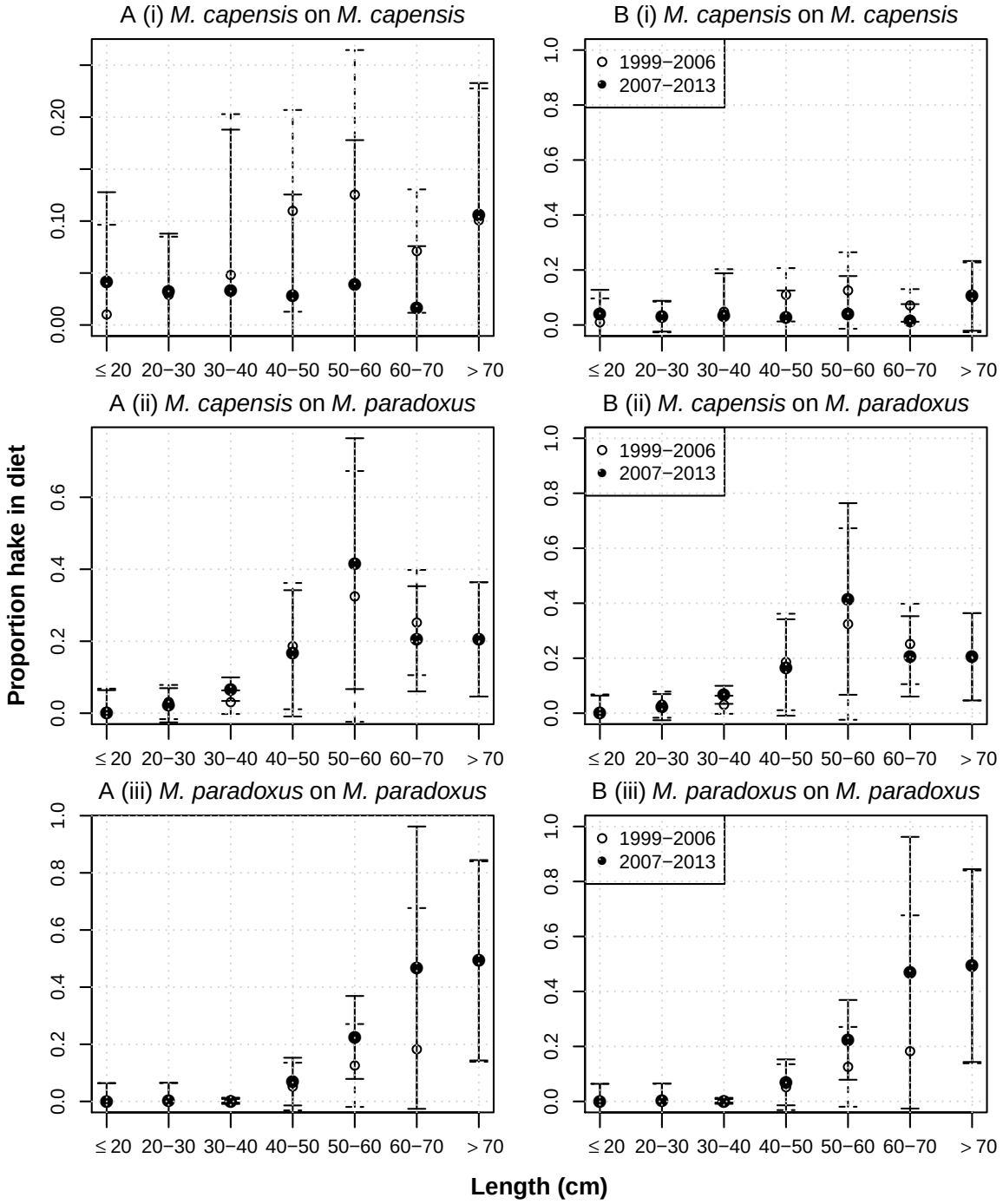


Figure 5.B.3: Proportion of hake in the hake diet estimated using data for the years 1999-2006 and for the years 2007-2013 separately. Column A on the left and column B on the right show the same information but with different vertical axis scales. Scales for column A were chosen to best show the temporal differences for each predator/prey pairing, while column B has the same scale for readier comparison across these pairings.

5.C Bounds on biologically feasible values for the daily ration

Since no direct experiments have been conducted for Cape hake to determine daily ration, this information needs to be drawn from elsewhere. Essington *et al.* (2001) propose that since the von Bertalanffy growth function is based on the bioenergetics of fish growth, it should be possible to estimate consumption rates from size-at-age data. Essington *et al.* (2001) express growth rate, in terms of change in mass over time, as follows:

$$\frac{dw_t}{dt} = H(w_t)^d - K(w_t)^n \tag{5.C.1}$$

where

w_t	is the weight of a fish aged t years,
$H(w_t)^d$	reflects the total rate of energy assimilation, and
$K(w_t)^n$	represents the energy losses.

For mathematical convenience, Essington *et al.* (2001) go on to make the assumption that $n = 1$, allowing Equation 5.C.1 to be integrated:

$$w_t = w_\infty \left(1 - \exp\left(-K(1-d)(t-t_0)\right)\right)^{1/(1-d)} \tag{5.C.2}$$

where

t_0	is the age at which weight is zero, and
w_∞	is the asymptotic weight, which can be found by setting $dw_t/dt = 0$:

$$w_\infty = (H/K)^{1/(1-d)} \tag{5.C.3}$$

Substituting the weight-length relationship $w_t = al^b$ into Equation 5.C.2, the following relationship is derived for length l_t:

$$l_t = l_\infty \left(1 - \exp\left(-K(1-d)(t-t_0)\right)\right)^{1/b(1-d)} \tag{5.C.4}$$

When $d = 2/3$ and $b = 3$, Equation 5.C.4 becomes the von Bertalanffy equation in its well-known form :

$$l_t = l_\infty \left(1 - \exp\left(-\kappa(t-t_0)\right)\right) \tag{5.C.5}$$

where $\kappa = K/3$.

Now consumption rate (mass per year) can be derived from the assimilation rate by $C = (H/A)w_t^d$, where A is the assimilation efficiency. Let δ^{ration} be the daily ration as a percentage of body mass. This can then be expressed as:

$$\delta^{ration} = C/w_t = (H/A)w_t^{d-1}\left(\frac{1}{365}\right)(100) \tag{5.C.6}$$

Given that

$H = Kw_\infty^{1-d}$	(from Equation 5.C.3),
$d = 2/3$	(assumption),
$b = 3$	(assumption, but in fact very close to the hake weight-length relationship values of 3.113 for *M. capensis* and 3.046 for *M. paradoxus*), and
$K = 3(\kappa)$	(from Equation 5.C.5 with κ specified from the von Bertalanffy growth curve for hakes),

hypothetical values for daily ration can be derived by making assumptions about the assimilation efficiency A. This has been carried out using two methods: (1) by using Equation 5.C.6 directly with the growth curve parameters from the assessment model, and (2) by estimating the parameters of the weight-based version of the von Bertalanffy growth curve (Equation 5.C.2) by fitting to hake size-at-age data.

5.C.1 Method 1: Calculate from Equation 5.C.6

Table 5.C.1 shows the estimates of daily ration that result for various values of the assimilation efficiency A. The growth curve parameters assumed are the estimates from the Rademeyer and Butterworth (2014b) reference case, provided in Table 4.2. The daily rations range from 0.05 to 4.59% of body mass, depending on the value of the assimilation efficiency.

5.C.2 Method 2: Estimate parameters from hake size-at-age data

The Rademeyer and Butterworth (2014b) model fits to size-at-age data to estimate hake growth curve parameters. To obtain estimates of daily ration, the weight-based Equation 5.C.2 rather than the standard length-based Equation 5.C.5 can be fit to these size-at-age data. This was done in two ways: first by estimating the w_∞, t_0, K and d parameters (results are shown in Table 5.C.2), and secondly by fixing d at 2/3, K at a series of values, and estimating w_∞ and t_0 (results are shown in Table 5.C.3). In each case, results are shown for a selection of three values for the assimilation efficiency A (0.3, 0.5 and 0.7).

The results in Table 5.C.2 are shown for fits to the species- and sex-disaggregated data, as well as species- and sex-aggregated data. Daily ration values range from 0.22 to 8.08% across all the A values, and from 0.31 to 4.85% for $A = 0.5$.

There is, however, a definite confounding between the w_∞ and K parameters, since a larger value for one can be compensated by a smaller value of the other and *vice versa*. This led to the analyses of Table 5.C.3, which fixed d at the von Bertalanffy assumption of 2/3 and fixed K at various values. The K with the best negative log-likelihood ($K = 0.3$), yielded daily rations ranging from 0.15 to 2.44% of body mass.

5.C.3 Final choice of the bounds for the daily ration

As can be seen from these Tables, the estimates of daily ration can vary substantially depending on the assumed value for the assimilation efficiency, A. Essington *et al.* (2001) assume a value of 0.65 for A in their analyses of data for bluefin tuna (*Thunnus thynnus*) and yellowfin tuna (*Thunnus albacares*), while Speirs *et al.* (2010) assume a value for A of 0.6 for cod, haddock and whiting. Even if A is assumed to be around 0.6, the daily rations estimated in the analyses of this Appendix still span a relatively large range (roughly 0.09% to 4% across the three Tables). Bearing this range in mind, as well as the daily rations listed in Table 2.3 of Chapter 2, lower and upper bounds for daily ration of 0.1 and 4% of body mass seem reasonable.

5.C.4 Daily ration as a function of fish weight

A further useful aspect of the Essington *et al.* (2001) work is that it provides a relationship between daily ration and fish weight (Equation 5.C.6), providing an indication of how the quantity of food consumed by fish should change with age: a regression of $ln\delta^{ration}$ against lnw_t should yield a slope of $d - 1 = -\frac{1}{3}$.

Table 5.C.1: Daily ration as a percentage of body mass, as estimated by the Essington *et al.* (2001) Method 1 (see text), for various assimilation efficiency rates A. Note that the zero age group has not been included here since the predation model considers predators from age 1 and up only.

M. paradoxus															
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Length (cm)	16.05	24.87	33.70	42.52	51.34	60.17	68.99	77.81	86.63	95.46	104.28	113.10	121.92	130.74	139.56
Weight (g)	29	111	279	566	1006	1630	2474	3569	4950	6651	8705	11148	14014	17336	21150
A	Daily ration as a percentage of body weight														
0.1	4.59	2.96	2.19	1.73	1.43	1.22	1.07	0.95	0.85	0.77	0.71	0.65	0.60	0.56	0.53
0.2	2.30	1.48	1.09	0.87	0.72	0.61	0.53	0.47	0.43	0.39	0.35	0.33	0.30	0.28	0.26
0.3	1.53	0.99	0.73	0.58	0.48	0.41	0.36	0.32	0.28	0.26	0.24	0.22	0.20	0.19	0.18
0.4	1.15	0.74	0.55	0.43	0.36	0.31	0.27	0.24	0.21	0.19	0.18	0.16	0.15	0.14	0.13
0.5	0.92	0.59	0.44	0.35	0.29	0.24	0.21	0.19	0.17	0.15	0.14	0.13	0.12	0.11	0.11
0.6	0.77	0.49	0.36	0.29	0.24	0.20	0.18	0.16	0.14	0.13	0.12	0.11	0.10	0.09	0.09
0.7	0.66	0.42	0.31	0.25	0.20	0.17	0.15	0.14	0.12	0.11	0.10	0.09	0.09	0.08	0.08
0.8	0.57	0.37	0.27	0.22	0.18	0.15	0.13	0.12	0.11	0.10	0.09	0.08	0.08	0.07	0.07
0.9	0.51	0.33	0.24	0.19	0.16	0.14	0.12	0.11	0.09	0.09	0.08	0.07	0.07	0.06	0.06
1	0.46	0.30	0.22	0.17	0.14	0.12	0.11	0.09	0.09	0.08	0.07	0.07	0.06	0.06	0.05
M. capensis															
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Length (cm)	15.58	23.92	32.27	40.62	48.96	57.31	65.65	74.00	82.34	90.68	99.03	107.37	115.71	124.05	132.39
Weight (g)	26	98	249	509	911	1487	2270	3295	4595	6205	8161	10498	13251	16457	20153
A	Daily ration as a percentage of body weight														
0.1	4.57	2.98	2.21	1.75	1.45	1.24	1.08	0.96	0.86	0.79	0.72	0.66	0.62	0.57	0.54
0.2	2.29	1.49	1.10	0.88	0.73	0.62	0.54	0.48	0.43	0.39	0.36	0.33	0.31	0.29	0.27
0.3	1.52	0.99	0.74	0.58	0.48	0.41	0.36	0.32	0.29	0.26	0.24	0.22	0.21	0.19	0.18
0.4	1.14	0.74	0.55	0.44	0.36	0.31	0.27	0.24	0.22	0.20	0.18	0.17	0.15	0.14	0.13
0.5	0.91	0.60	0.44	0.35	0.29	0.25	0.22	0.19	0.17	0.16	0.14	0.13	0.12	0.11	0.11
0.6	0.76	0.50	0.37	0.29	0.24	0.21	0.18	0.16	0.14	0.13	0.12	0.11	0.10	0.10	0.09
0.7	0.65	0.43	0.32	0.25	0.21	0.18	0.15	0.14	0.12	0.11	0.10	0.09	0.09	0.08	0.08
0.8	0.57	0.37	0.28	0.22	0.18	0.16	0.14	0.12	0.11	0.10	0.09	0.08	0.08	0.07	0.07
0.9	0.51	0.33	0.25	0.19	0.16	0.14	0.12	0.11	0.10	0.09	0.08	0.07	0.07	0.06	0.06
1	0.46	0.30	0.22	0.18	0.15	0.12	0.11	0.10	0.09	0.08	0.07	0.07	0.06	0.06	0.05

Table 5.C.2: Daily ration as a percentage of body mass, as estimated by the Essington *et al.* (2001) Method 2 (see text), with d and K estimated. Results are shown for a selection of three values of the assimilation efficiency rate A. Thanks go to R. Rademeyer for setting up the ADMB code for these analyses.

	M. paradoxus males			*M. paradoxus* females			*M. capensis* males			*M. capensis* females			Aggregated		
Variable	value	std.dev		value	std.dev		value	std.dev		value	std.dev		value	std.dev	
lnw_∞	10.051	0.656		11.000	0.002		11.000	0.002		9.915	0.189		10.038	0.166	
t_0	-9.467	25.070		-3.571	2.527		-3.571	2.527		-10.000	0.007		-10.000	0.094	
d	0.967	0.178		0.817	0.090		0.817	0.090		0.976	0.004		0.971	0.003	
K	5.143	30.667		0.439	0.303		0.439	0.303		7.702	1.894		5.830	1.065	
Daily ration as a percentage of body weight															
Age	A=0.3	A=0.5	A=0.7	A=0.3	A=0.5	A=0.7	A=0.3	A=0.5	A=0.7	A=0.3	A=0.5	A=0.7	A=0.3	A=0.5	A=0.7
1	1.17	0.70	0.50	1.30	0.78	0.56	1.30	0.78	0.56	8.08	4.85	3.46	6.30	3.78	2.70
2	1.13	0.68	0.48	1.11	0.67	0.48	1.11	0.67	0.48	7.88	4.73	3.38	6.13	3.68	2.63
3	1.10	0.66	0.47	0.98	0.59	0.42	0.98	0.59	0.42	7.72	4.63	3.31	5.99	3.59	2.57
4	1.08	0.65	0.46	0.88	0.53	0.38	0.88	0.53	0.38	7.60	4.56	3.26	5.87	3.52	2.52
5	1.06	0.63	0.45	0.81	0.48	0.35	0.81	0.48	0.35	7.50	4.50	3.21	5.78	3.47	2.48
6	1.04	0.62	0.45	0.75	0.45	0.32	0.75	0.45	0.32	7.41	4.45	3.18	5.71	3.42	2.45
7	1.03	0.62	0.44	0.70	0.42	0.30	0.70	0.42	0.30	7.35	4.41	3.15	5.64	3.39	2.42
8	1.02	0.61	0.44	0.66	0.40	0.28	0.66	0.40	0.28	7.29	4.37	3.12	5.59	3.35	2.40
9	1.01	0.61	0.43	0.63	0.38	0.27	0.63	0.38	0.27	7.25	4.35	3.11	5.55	3.33	2.38
10	1.00	0.60	0.43	0.60	0.36	0.26	0.60	0.36	0.26	7.21	4.33	3.09	5.51	3.31	2.36
11	1.00	0.60	0.43	0.58	0.35	0.25	0.58	0.35	0.25	7.18	4.31	3.08	5.48	3.29	2.35
12	0.99	0.59	0.42	0.56	0.34	0.24	0.56	0.34	0.24	7.15	4.29	3.07	5.46	3.27	2.34
13	0.99	0.59	0.42	0.54	0.33	0.23	0.54	0.33	0.23	7.13	4.28	3.06	5.44	3.26	2.33
14	0.98	0.59	0.42	0.53	0.32	0.23	0.53	0.32	0.23	7.12	4.27	3.05	5.42	3.25	2.32
15	0.98	0.59	0.42	0.52	0.31	0.22	0.52	0.31	0.22	7.10	4.26	3.04	5.40	3.24	2.32

Table 5.C.3: Daily ration as a percentage of body mass, as estimated by the Essington *et al.* (2001) Method 2, with d fixed at 2/3 and K fixed at a range of values. Results are shown for a selection of three values of the assimilation efficiency rate A. The total negative log-likelihood has been shown for each choice of K. Thanks go to R. Rademeyer for setting up the ADMB code for these analyses.

	$K = 0.1$ $(-lnL = 406.90)$			$K = 0.3$ $(-lnL = 405.97)$			$K = 0.5$ $(-lnL = 408.97)$			$K = 0.9$ $(-lnL = 424.59)$		
Variable	value	std.dev		value	std.dev		value	std.dev		value	std.dev	
lnw_∞	12.364	0.051		9.930	0.039		9.066	0.032		8.310	0.025	
t_0	-0.909	0.093		-0.191	0.069		0.301	0.055		0.934	0.039	
d (fixed)	2/3			2/3			2/3			2/3		
K (fixed)	0.1			0.3			0.5			0.9		
Daily ration as a percentage of body weight												
Age	A=0.3	A=0.5	A=0.7	A=0.3	A=0.5	A=0.7	A=0.3	A=0.5	A=0.7	A=0.3	A=0.5	A=0.7
1	1.48	0.89	0.63	2.44	1.46	1.05	4.15	2.49	1.78	41.70	25.02	17.87
2	0.99	0.59	0.42	1.39	0.84	0.60	1.85	1.11	0.79	3.00	1.80	1.29
3	0.75	0.45	0.32	1.00	0.60	0.43	1.26	0.76	0.54	1.78	1.07	0.76
4	0.60	0.36	0.26	0.80	0.48	0.34	0.99	0.60	0.43	1.37	0.82	0.59
5	0.51	0.31	0.22	0.68	0.41	0.29	0.84	0.50	0.36	1.17	0.70	0.50
6	0.44	0.27	0.19	0.59	0.36	0.25	0.74	0.45	0.32	1.05	0.63	0.45
7	0.39	0.24	0.17	0.53	0.32	0.23	0.68	0.41	0.29	0.98	0.59	0.42
8	0.36	0.21	0.15	0.49	0.29	0.21	0.63	0.38	0.27	0.93	0.56	0.40
9	0.32	0.19	0.14	0.46	0.27	0.20	0.60	0.36	0.26	0.90	0.54	0.39
10	0.30	0.18	0.13	0.43	0.26	0.18	0.57	0.34	0.24	0.88	0.53	0.38
11	0.28	0.17	0.12	0.41	0.24	0.17	0.55	0.33	0.24	0.86	0.52	0.37
12	0.26	0.16	0.11	0.39	0.23	0.17	0.53	0.32	0.23	0.85	0.51	0.37
13	0.25	0.15	0.11	0.37	0.22	0.16	0.52	0.31	0.22	0.84	0.51	0.36
14	0.23	0.14	0.10	0.36	0.22	0.15	0.51	0.31	0.22	0.84	0.50	0.36
15	0.22	0.13	0.10	0.35	0.21	0.15	0.50	0.30	0.21	0.83	0.50	0.36

5.D The shift of *M. capensis* predator preference for *M. capensis versus M. paradoxus* prey with depth

The preference that a hake predator of a given size exhibits for hake prey of different sizes will be a function of both the predator to prey size ratio and the availability of the prey. It seems reasonable to assume that the inherent size preference that hake predators exhibit for hake prey will not change (on average) with depth, but since hake move into deeper water as they grow older, and in particular *M. capensis* predators start to encounter small *M. paradoxus* prey more frequently, the dynamics of the prey availability is likely to change with depth. This appendix concerns itself particularly with the question of to what extent *M. capensis* preference would shift from *M. capensis* to *M. paradoxus* as these predators move into deeper water.

Figure 5.D.1 plots the prey length to predator length ratios derived from the samples of the 1999-2013 DAFF biological dataset. The data have been aggregated for all depth strata and predator and prey sizes in order to get an overall impression of this predator-prey size preference. As can be seen from this Figure, hake predators tend to prefer prey that is about 40% of predator size, with the majority of prey lengths falling between 22% and 60% of predator length. This Figure also shows that on average the *M. capensis* prey is slightly larger than *M. paradoxus* prey for *M. capensis* predators. Let the term "preferred" prey be used below to denote prey with lengths that fall within the 22% to 60% range of predator length.

Bearing this observation in mind, it would be useful to determine at which depths the most "preferred" hake prey is likely to be found for a predator of a given size in relation to the predator's own depth-distribution, in order to be able to infer how the *M. capensis* preference might shift from *M. capensis* to *M. paradoxus* prey with depth. The DAFF biological data set is a sub-set of the research survey data which were made available for the analyses of Appendix 3.A (T. Fairweather, *pers. comm.*). This bigger dataset provides information on the depth distributions of hake of different sizes, as well as the overlap between predators and potential prey and has been analysed to get an estimate of the proportion of "preferred" prey that a predator might encounter in each depth stratum, as described below.

For a given predator species s_p and age a_p, and a given depth stratum d, first the expected length of the predator, l_p, is calculated from the von Bertalnffy growth curve, and secondly all the samples are extracted from the survey data set that (a) were collected in the same depth stratum and (b) for which the length is less than l_p. This subset represents a sample of the "potential" hake prey for a predator of species s_p and age a_p in depth stratum d. For *M. capensis* predators this subset would consist of both *M. capensis* and *M. paradoxus* prey, while for *M. paradoxus* of only *M. paradoxus* prey. From this sample of "potential" prey, the number of "preferred" prey is extracted by considering only those samples for which the prey to predator length ratio lies between 22% and 60%. In the case of *M. capensis* predators, this number is extracted separately for *M. capensis* and *M. paradoxus* prey. Thus the proportion of the total "potential" hake prey that consists of "preferred" *M. capensis* and "preferred" *M. paradoxus* prey can be calculated for each depth stratum.

These proportions are shown in Figure 5.D.2 along with a measure of predator abundance given by the total number of samples in the survey dataset of species s_p and age a_p (expected ages are again calculated from the lengths of the samples) in each depth stratum d. In this Figure it can be seen that as a *M. capensis* predator grows larger (and moves into deeper water), the overlap with "preferred" prey shifts from *M. capensis* to *M. paradoxus*. So while a large *M. capensis* predator may have a high preference in "theory" for small *M. capensis* prey, the latter are mostly found in the shallower waters, where the large *M. capensis* predators are low in abundance, so that the effective preference is much lower.

While the main focus of this appendix is the shift in preference for *M. capensis* predators, the corresponding results for *M. paradoxus* predators have been included in the interest of completeness. It should be noted when interpreting the results shown in Figure 5.D.2 that only the proportions and not the total samples sizes are shown for each depth stratum. Thus the bars across the depth strata for a given age bear no direct relationship to one another, and some bars may correspond to small sample sizes.

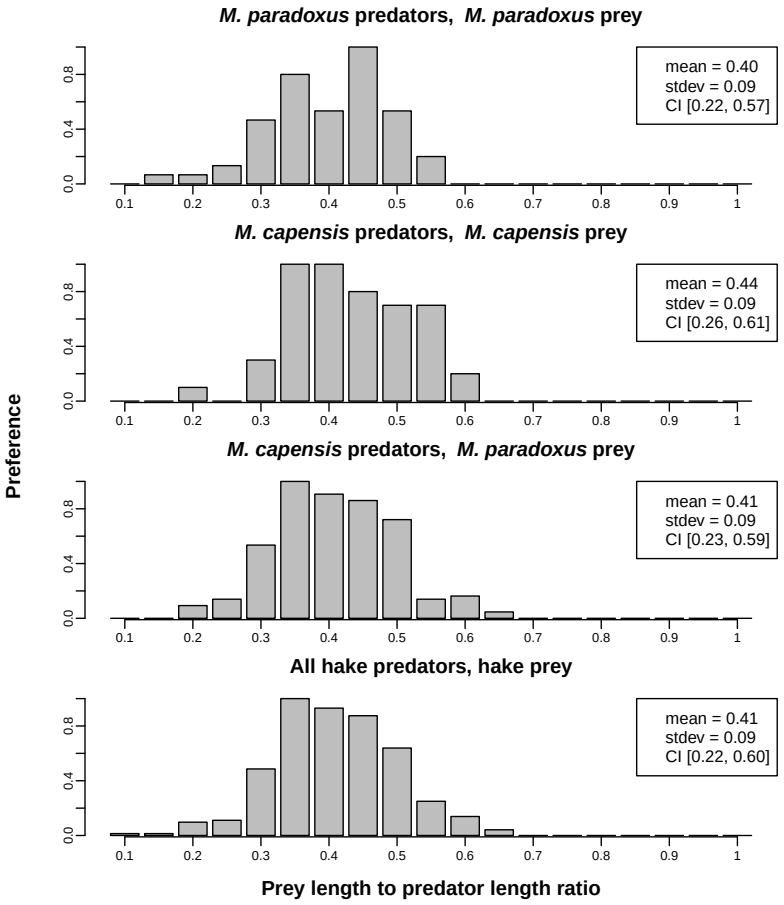


Figure 5.D.1: The distributions of hake prey length to predator length ratios from the stomach content samples of the DAFF 1999-2013 biological dataset are shown for *M. capensis* and *M. paradoxus* predators separately, and for both species combined. The mean, standard deviation and 95% confidence interval (twice the standard deviation from the mean) for the each distribution are shown in the corresponding legend.

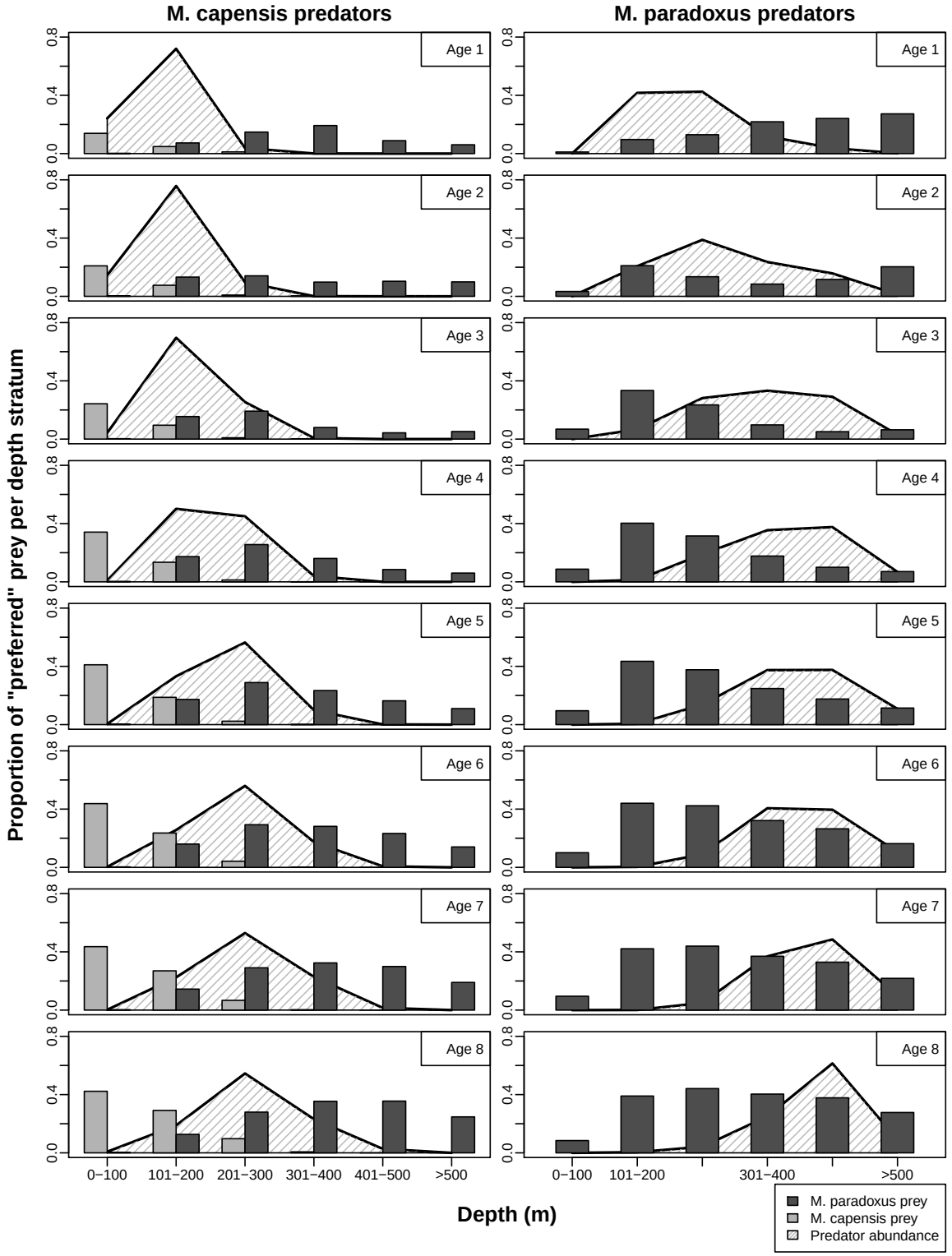


Figure 5.D.2: The proportion of "preferred" hake prey available in different depth strata is shown for predators of different species and ages. For a given predator age a_p, prey species s and depth stratum d, this proportion of "preferred" prey is the proportion of the total "potential" prey in stratum d for which the prey length is between 22% and 60% of the predator length. "Potential" prey simply means all samples in the survey dataset of hake species s collected in depth stratum d for which the recorded length is less than the expected length of a predator of age a_p. Light grey bars correspond to *M. capensis* prey and dark grey bars to *M. paradoxus* prey. The striped area provides a measure of the relative abundance of the predator at different depths, given by the total number of samples of predators of that age collected in the surveys.

Chapter 6

Results and Discussion

6.1 Introduction

This Chapter presents the results of the main analyses and sensitivities for the predation model developed in this thesis. Detailed presentations of the results are provided in the sections that follow, but an overview of the overall structure is given here first, since references to the various Tables and Figures are made throughout this Chapter. First, results are presented for the models from the base case development phase, during which adjustments and additional constraints were imposed on the predation model to develop what is presented as the base case in this thesis. Secondly, a full set of results is presented for the base case, with comparisons to the Rademeyer and Butterworth (2014b) model, as well as to a variant of the predation model with the predation "off" (more details about this are given later). Finally, results for the sets of sensitivity runs are presented, the details of which are also provided later.

Table 6.1a (*M. paradoxus*) and Table 6.1b (*M. capensis*) list key model outputs, consisting of various measures of spawning biomass, for all the runs presented in this Chapter. First, biomass is given in absolute terms for the pre-exploitation equilibrium (K^{sp}) and for 2013 (B^{sp}_{2013}), the last year considered in the model. Secondly, the biomass for the years 1977, 2007 and 2013 are given relative to the pre-exploitation biomass. The years 1977 and 2007 have been included since these are the years for which particularly low catch rates were reported for the fishery. Thirdly, the maximum and minimum biomasses (relative to K^{sp}) are listed together with the years in which they occurred. Finally, the proportional reduction in the model-estimated ICSEAF CPUE series (see Equation 4.27) from 1955 to 1977 is reported along with the difference to the corresponding reduction in the observed CPUE. All of these measures of biomass correspond to key features in the exploitation history of the hake resources and will be discussed further later. Table 6.2 provides precision esimates for a selection of key model outputs from Tables 6.1a and 6.1b.

Table 6.3 gives the negative log-likelihoods for all the runs, first as totals including and excluding penalties. The negative log-likelihoods are then broken down into a non-predation component (all likelihood contributions from Chapter 4 that are not penalties), a predation component (all likelihood contributions from Chapter 5 that are not penalties) and a penalty component. These penalties include penalties for survey selectivity smoothing (Equation 4.25), new survey gear (Equation 4.42), and the catches (Equation 4.49). Where applicable, further diet-related penalties include penalties for the limits on daily ration (Equation 5.32), the slope of daily ration with predator weight (Equation 5.36), a posfun penalty for the implementation of P_{lim}, a penalty to force the

daily ration of hake aged 3 (Equation 6.2) and a penalty to force the *M. paradoxus* depletion level (Equation 6.3). The last three sections of Table 6.3 give the respective negative log-likelihood components for the CPUE, catch-at-length and diet data.

Table 6.4 gives the estimates for the parameters of the non-predation component of the model (see also Table 4.7 of Chapter 4), and Table 6.5 lists the estimates for the predation-related components of the model (see also Table 5.1 of Chapter 5).

Tables 6.6a and 6.6b give the breakdown by predator and prey age and species of the total number of hake consumed in the years 1916 and 2013 respectively, as estimated in the base case model. Tables 6.7a and 6.7b list the base case estimates of the daily per capita consumption of hake prey by hake predators for the years 1916 and 2013 respectively.

Note that in the discussions that follow, "daily ration" is taken to refer to "daily ration as a percentage of body mass".

6.2 Base case development

This section deals with the model refinements that were necessary to develop the model that has been chosen as the base case for the results presented in this thesis.

***No constraints on daily ration* (Figure 6.1)**

The first model for which results are shown imposes no constraints on daily ration. In Figure 6.1, this is the run marked as "No DR constraint" (where DR is an abbreviation for daily ration), with the dark blue lines. The four plots in Block A of this Figure show the spawning biomasses for the two hake species in absolute terms and relative to pre-exploitation biomass. For each of these four plots, the Rademeyer and Butterworth (2014b) spawning biomass trajectory has been included for comparison purposes[1]. The most marked difference between the Rademeyer and Butterworth (2014b) model and this predation model with no constraints on daily ration is that the *M. paradoxus* spawning biomass trajectory starts to increase above carrying capacity as the population size of its major predator, *M. capensis*, is reduced by the fishery, peaking in the year 1958 at a level over 50% higher than the *M. paradoxus* pre-exploitation level (see Table 6.1a). This predation release of *M. paradoxus* is a constant feature (with varying magnitude) in all the hake models that take predation into account. The predation model also reflects a much lower pre-exploitation spawning biomass in absolute terms than the Rademeyer and Butterworth (2014b) model.

It is interesting to note that the *M. capensis* population exhibits an increase in biomass in the 1960s. This may largely be a result of decreasing *M. capensis* catches as the fishery moved its focus to *M. paradoxus*, but since this increase is not evident (to the same extent) in the Rademeyer and Butterworth (2014b) non-predation model, there could be an element of predation release for *M. capensis* as well following the fishing of large *M. capensis*, which of course cannibalise small *M. capensis*.

The predation model achieved a reasonable fit to the CPUE data (Block B), but estimated an unrealistically low daily ration for *M. paradoxus* predators (Block C, with a maximum of 0.3% going all the way down to 0.01%).

[1] Note in this Figure, and all other Figures in this Chapter, the term "Rademeyer model" has been used to refer to the Rademeyer and Butterworth (2014b) model, in order to make efficient use of space in the Figures.

Furthermore, the estimated proportions of *M. capensis* hake in the diet of *M. capensis* predators (Block D) lie below the averages estimated from the diet data, although still within the 95% confidence intervals.

Introducing bounds on daily ration **(Figure 6.1)**

The very low *M. paradoxus* daily rations estimated in the previous model show that without any information on daily ration, the best fit of the hake predation model does not provide biologically feasible estimates for these rations. The second model presented in Figure 6.1 (light blue lines) thus introduces a lower bound of 0.1% and an upper bound of 4.0% on the daily rations, which are considered to be biologically realistic bounds (see Section 5.5.1 and Appendix 5.C).

The daily rations estimated for *M. paradoxus* by this second model are still very low on the whole, but lie within the specified bounds. Thus, while the results may not appeal from a biological perspective (one would, for example, expect younger hake to consume a higher daily ration as a percentage of body mass; see Durbin *et al.* 1983, Griffiths *et al.* 2009), they would strictly speaking be considered acceptable in terms of the conditions for the daily ration imposed on the model.

It is interesting to note that with the higher daily ration of older *M. paradoxus* hake (and as a matter of fact of older *M. capensis* hake), the *M. paradoxus* trajectory (Block A) exhibits oscillations of greater amplitude, shows a greater predation release (peaking in 1958 at double the pre-exploitation biomass, see Table 6.1a) and is currently less depleted than the previous model (46% of pre-exploitation biomass in contrast to 13% estimated previously; see Table 6.1a). These oscillations and lower depletion levels are, however, accompanied by a slightly worse fit to the historical ICSEAF CPUE data (with a loss of 7.5 log-likelihood points; see Table 6.3). Furthermore, the model-estimated historical CPUE indices show drop of only 55% between 1955 and 1977 (in contrast to the drop of 72% in the observed data). Thus, on the whole, the fit to the historical CPUE data is rather worse, although the biomass trajectories do still show a relatively high extent of depletion (by comparison to surrounding years) in 1977 and 2007, the two years for which the fishery suffered from low catch rates.

A further aspect of concern is that this model still battles to fit the proportion of *M. capensis* prey in the diet of *M. capensis* predators. In particular, it is the smaller *M. capensis* predators that do not consume enough *M. capensis* prey in the model. In reality, owing to geographic overlap (or lack thereof), small hake are more likely to consume *M. capensis* prey, while larger hake will feed more extensively on *M. paradoxus* prey (as illustrated in Appendix 5.D). The lack of fit to these proportions thus likely arises from the fact that the model as developed thus far has no means of allowing *M. capensis* predators to shift their preference from *M. capensis* to *M. paradoxus* prey as they grow older.

Introducing a depth availability vector **(Figure 6.2)**

In light of this last observation, this next refinement of the model introduces a depth availability vector that allows this shift in *M. capensis* preference from *M. capensis* prey to *M. paradoxus* prey (see Section 5.5.2). The results of this model are given in Figure 6.2, and immediately show an improvement not only in the proportion of *M. capensis* prey in the diet of *M. capensis* predators, but also in the fit to the historical CPUE data. For this model, however, these improvements come at the expense of not only a lower *M. paradoxus* daily ration, but also a daily ration that is relatively constant with age for *M. paradoxus*, as can be seen by the slope of the log-regression of daily ration against body mass reported under the legends of Block C. Correcting this feature leads to the penultimate model refinement in the base case development stage:

Constraining the slope of the daily ration with predator weight **(Figure 6.2)**

The second model shown in Figure 6.2 adds a penalty to the negative log-likelihood to force the slope of the log of the daily ration against the log of the body mass to lie close to -1/3 (see Section 5.5.3). The results of this latest refinement are very similar to the previous model (compare the purple and dark blue lines in Figure 6.2), except for some changes in the daily ration estimates. The *M. capensis* daily ration is lower on the whole (but still reasonable). The *M. paradoxus* daily ration, however, is substantially higher for lower ages, but shows a very rapid drop in daily ration for predators aged 3 and above. This sharp drop may be a compensation arising from the general trait shown by the model that a higher daily ration for older *M. paradoxus* predators is linked with a worse fit to the historical CPUE data (see for example the two models in Figure 6.1).

Limiting the predation mortality rate: introducing competition **(Figure 6.2)**

The link between a higher daily ration and population oscillations of greater amplitude (leading to a worse fit to the historical CPUE data) is the predation mortality rate. Given that a (usually quite large) proportion of a hake predator's diet consists of hake, it follows naturally that the higher the daily ration is, the more hake will be consumed and the higher the predation mortality rate for the hake prey will be. A high mortality rate will lead to greater fluctuations in the population size, as the population consequently responds more quickly to changes in predation and fishing pressures.

The predation mortality rates have not been shown for all the development and sensitivity models, but in the "DR limit" model from Figures 6.1 (and 6.2), for example, for which the *M. paradoxus* population trajectory exhibits greater fluctuations, the total natural mortality rate (including predation) at pre-exploitation equilibrium is nearly 1.2 yr^{-1} for hake between the ages 1 and 5 (roughly 16—50cm in length). Even for the previous "Slope DR" model in Figure 6.2, the pre-exploitation total natural mortality rates for *M. paradoxus* are over 1.0 yr^{-1} for hake between the ages of 3 and 5 (roughly 30—50cm in length). These mortality rates are substantially higher than those assumed in the Rademeyer and Butterworth (2014b) model (0.75 yr^{-1} for hake of age 2 and less, decreasing linearly to 0.375 yr^{-1} for hake aged 5 and above, or hake of roughly 50cm and longer) and can lead to instabilities in the population's dynamics.

Punt (1994)introduces a term which reduces consumption as predator density increases (to reflect the effect of possible competition amongst predators). Koen-Alonso and Yodzis (2005) point out that such a competition effect is likely to be a common feature in natural populations, since competition between predators is likely to reduce their efficiency in hunting hake prey if the predator cohort is large, and furthermore found that the incorporation of a competition term greatly improved the performance of the models.

A competition element was introduced to this predation model by simply limiting the maximum monthly predation mortality rate to a fixed value, P_{lim}. Figures 6.3 and 6.4 present the results for five different values of P_{lim}. Figure 6.3 shows the results for when no P_{lim} is enforced (which is the same as the "Slope DR" model from the previous Figure) and for $P_{lim} = 0.07$[2] and for $P_{lim} = 0.05$. These two P_{lim} models are shown together in this Figure as they seem to be examples of runs that exhibit "switching". More discussion on this will follow later in Section 6.4. Figure 6.4 shows the results for the no P_{lim} (Slope DR") model again, along with $P_{lim} = 0.06$, $P_{lim} = 0.04$ and $P_{lim} = 0.03$. The trends in Figure 6.4 show that the lower the value of P_{lim}, the lower the daily ration (for both species), the less the extent of predation release exhibited by *M. paradoxus* (and in fact by *M. capensis* in the 1960s) and the better the fit to the historical CPUE data (except for a slightly

[2]Note that since this P_{lim} is a restriction on the monthly predation rate, $P_{lim} = 0.07$ effectively limits the annual predation rate to 0.84 yr^{-1}.

worse fit to the South Coast historical CPUE for $P_{lim} = 0.06$). The results in fact approach the results of the predation model when it is run with predation "off" (see Section 6.3 for more details on this run), which is to be expected since the imposition of a P_{lim} constraint effectively scales down the effect of the predation.

Final selection of the base case

The results of Figures 6.3 and 6.4 suggest that if P_{lim} is too low, then the daily rations are substantially reduced and the predation effect is essentially removed from the model, but if P_{lim} is too high, then the model can manifest instabilities. The model run with an intermediate $P_{lim} = 0.06$ (corresponding to an annual predation rate of 0.72 yr^{-1}) was thus chosen as the base case model for this thesis. Note that $P_{lim} = 0.05$ and $P_{lim} = 0.07$ were not chosen since they exhibit "switching" (see Section 6.4).

An important point to note is that the (negative) log-likelihood values in Table 6.3 have had relatively little role in the development process and choice of this final base case. This is largely because there is insufficient information in the data to estimate age-specific daily rations (even when bounds and slopes are imposed), so that the assessment of what constitutes a "good overall fit" becomes a somewhat qualitative judgement. Furthermore, different runs can switch between favouring different likelihood components (see Section 6.4), making it difficult to chose a base case based on maximum (penalised) likelihood alone. This is more so when there are conflicts to some extent amongst the various data, and the specifications for their different weightings in the log-likelihood are not that clearly determinable. In the future, if the predation model is to be used as a basis to provide management advice, a Reference Set of different variants of the model would need to be developed so that the management advice takes account of major uncertainties in the model.

6.3 Base case

Figures 6.5a to 6.5n present the full set of results for the base case model. Figure 6.5a shows the spawning biomass trajectories in absolute terms and relative to the pre-exploitation equilibrium spawning biomasses. In this Figure, the trajectories are shown for three models: the base case predation model, the Rademeyer and Butterworth (2014b) model and a model referred to as the predation "off" model. This last model is a variant of the predation model for which the predation mortality rates are set to zero, and the basal mortality rates are fixed at the values of the Rademeyer and Butterworth (2014b) natural mortality rates. This predation "off" model is still not identical to the Rademeyer and Butterworth (2014b) model; the difference are listed below:

Rademeyer and Butterworth (2014b) model	Predation "off" model
Sex-disaggregated	Sex-aggregated
Fits to age-length keys	Does not fit to age length keys
Modified Ricker stock-recruitment relationship	Beverton-Holt stock-recruitment relationship
Pope's approximation for the catch equation	Baranov formulation of the catch equation
Annual time-step	Monthly-time step

The spawning biomass trajectories estimated by these two non-predation models are very similar for *M. paradoxus*, but the predation "off" model estimates a higher *M. capensis* overall spawning biomass. The spawning biomasses relative to pristine biomass K^{sp}, however, show relatively comparable trajectories with differences that are well within the range of trajectories from the OMP-2014 reference set (see for example Figure 2 of Rademeyer and Butterworth 2014a). It should be born in mind that these assessment models generally perform better at estimating biomass trajectories in relative terms, rather than absolute, and as such the differences in

the *M. capensis* absolute spawning biomass between the Rademeyer and Butterworth (2014b) and the predation "off" model are not atypical.

Similar to the base case development models discussed in earlier sections, the base case predation model exhibits a predation release for the *M. paradoxus* population, peaking in 1958 at 1.3 times the pre-exploitation equilibrium spawning biomass. The *M. paradoxus* spawning biomass (relative to K^{sp}) then drops more rapidly than for the trajectories estimated by the non-predation models, but from the mid 1970s all three models show very similar trajectories. The *M. paradoxus* 2013 depletion level is 14%, which is marginally lower than the depletion levels estimated by the Rademeyer and Butterworth (2014b) model (18%) and the predation "off" model (15%)[3].

The *M. capensis* spawning biomass trajectory for the predation model shows an overall lower biomass (in absolute terms) than those estimated by the non-predation models and in contrast to the non-predation models exhibits some predation release in the 1960s, as has been noted previously. This increase in the *M. capensis* population in the 1960s is probably partly responsible for the more rapid decline in the *M. paradoxus* population (compared to the non-predation models) over the same period. All three models show reduced spawning biomasses for both species in the low catch rate years of 1977 and 2007 (although to a lesser extent in 1977 for the predation model).

Figure 6.5b shows the standardised stock-recruitment residuals estimated by the base case predation model and the two non-predation models. Information provided by the catch-at-length data allows for these residuals to be estimated by the models, and on the whole all three models estimate similar residuals, more so for *M. capensis*.

The top panel of Figure 6.5c shows the total natural mortality rates at pre-exploitation equilibrium for the predation model (which include the predation mortality rates), and compares these to the fixed natural mortality rates assumed in the Rademeyer and Butterworth (2014b) (and in the predation "off") model. It can be seen here that the natural mortality for the predation model is generally higher for hake up to the age of about 6. The effect of the P_{lim} constraint can be seen in particular in the *M. paradoxus* mortality rates, which have been truncated at 0.92 (which is $12P_{lim} + M^b$, where $P_{lim} = 0.06$ and $M^b = 0.2$). The bottom panel of Figure 6.5c provides a three dimensional plot of the predation mortality rates for each species. These plots illustrate the dependence of the predation mortality rate on the predator biomasses. For *M. paradoxus*, the predation mortality rates generally decrease as first the *M. capensis* and later the *M. paradoxus* population (i.e. the major predators of smaller *M. paradoxus*) were reduced, with some spikes in the late 1960s when the *M. capensis* population showed an increase. For the *M. capensis* population, the predation mortality rates similarly increase and decrease with increases and decreases in the *M. capensis* biomass trajectory.

Tables 6.6a and 6.6b give a breakdown (by predator and prey species and age) of the total number of hake consumed in the years 1916 and 2013. Tables 6.7a and 6.7b list the daily per capita consumption (by predator and prey species and age) of hake prey by hake predators (i.e. the number of hake of a given species and age consumed daily by hake of a given species and age). These four Tables provide an indication of which age-groups of hake predators are responsible for the most mortality on hake prey age-groups. It can be seen here, for example, that the plus-group of hake of age 15 and older are largely responsible for the relatively high predation mortality rates experienced by hake between the ages 3 and 7.

Figure 6.5d shows the same spawning biomasses relative to pre-exploitation spawning biomass as in Figure 6.5a, but contrasts the trajectories between the two species, as well as superimposing the trajectory for each species

[3]Confidence intervals have not been provided here because of the convergence challenges described later in this section. The main point to note here, however, is not whether or not the *M. paradoxus* depletion levels are significantly different, but rather that the inclusion of hake-on-hake predation and cannibalism does not substantially alter the overall perception of a *M. paradoxus* population well below its pre-exploitation abundance.

onto the total number of hake of that species consumed annually by hake predators, as well as onto the total catches taken for that species. This Figure illustrates how the *M. paradoxus* population increases in response to a decreasing *M. capensis* predator population in the first half of the 20th century as fishing commences on *M. capensis* (first panel) and then decreases as the level of fishing increases and extends to *M. paradoxus* in the second half (middle panel). These Figures also show that the increase in the *M. capensis* population in the 1960s is likely to have been caused by the decreasing catches of *M. capensis* around that time as the fishery moved offshore. However, as has been mentioned previously, the fact that this increase is not manifest in the non-predation model points to a predation release resulting from decreased *M. capensis* predators (and thus decreased cannibalism). The trends in the number of hake consumed are difficult to interpret since the consumption rate will be largely dependent on the relative sizes of the different predator and prey cohorts, and the Figure shows only the combined biomass.

Figures 6.5e and 6.5f show the fits to the commercial CPUE and survey biomass indices for the base case predation and the predation "off" model. The Rademeyer and Butterworth (2014b) fits have not been included here as they are very similar to the predation "off" fits. As can be seen from the plots as well as from the negative log-likelihoods in Table 6.3, the predation "off" model fits better to the historical CPUE data, but there is not much difference between the two models for the fits to the offshore CPUE data and to the survey biomass indices. The poorer fit to the historical ICSEAF CPUE data is a commonly occurring problem for the predation model, but for the base case model presented here the proportion to which the model estimate of the historical CPUE is reduced from 1955 to 1977 is 0.30, which is quite close to the reduction in the actual data.

Figures 6.5g and 6.5h show the fits to the commercial catch-at-length data for the predation and the predation "off" models. The first Figure shows the data and model fits for the individual years for which the data are available, and the second Figure shows the fits to the data averaged over each of the periods for which an unchanging selectivity function was estimated. Figures 6.5i and 6.5j show similar plots for the survey catch-at-length data, with Figure 6.5i showing the model fits and data for the individual years, and Figure 6.5i grouping the data into the years for which the old gear and the new gear were used in the surveys (and for which separate selectivities were estimated). The fits for the predation model and the predation "off" model to these data are generally quite good, although worse than the fits to the commercial catch-at-length data; possibly a reflection of sampling variability with low sample sizes on the surveys compared to the commercial fishery. The fits to the *M. capensis* South Coast commercial offshore catch-at-length data and the *M. paradoxus* South Coast spring survey catch-at-length data are poor, and the reasons for this lack of fit should be investigated in future work on the hake predation model. It is also evident that the fit to the commercial longline catch-at-length data (Figure 6.5h) is very good, so that the specification for the longline selectivity (which was simplified from the Rademeyer and Butterworth 2014b specifications) seems adequate.

The commercial selectivities estimated by the predation model, the predation "off" model and the Rademeyer and Butterworth (2014b) model are shown in Figure 6.5k. The commercial selevities are fairly similar for the three models, except that the West Coast offshore *M. paradoxus* selectivities for the Rademeyer and Butterworth (2014b) model have a distinct dome shape at older ages, whereas this is in most cases less evident in the predation and predation "off" models. Furthermore, the handline selectivity function for the predation and predation "off" model was set equal to the longline selectivity purely for convenience, while the Rademeyer and Butterworth (2014b) model takes this selectivity function to be the average between the South Coast longline and inshore selectivity parameters. This difference should be addressed in future work, but is unlikely to make a substantial difference since the handline catches constitute less than 3% of the total catch and occur over only a limited period (see Table 3.1).

The survey selectivities estimated by the same three models are shown in Figure 6.5l. The selectivities for the predation and predation "off" models are on the whole less smooth than for the Rademeyer and Butterworth (2014b) model, suggesting that the smoothing penalty (see Equation 4.25) may need to be given higher weight for these models. There is also a marked difference between the selectivities estimated for *M. paradoxus* for the South Coast spring surveys (the Rademeyer and Butterworth (2014b) model exhibiting a much steeper reduction at larger lengths), which may be the reason behind the worse fit to these data noted in Figure 6.5j and will need to be investigated further in the future.

Figure 6.5m shows (i) the fits of the predation model to the proportion of hake in the diet of hake predators, (ii) the model estimated daily rations as a percentage of body mass, and (iii) the shapes of the preference functions estimated by the model (see Equation 5.13). The fits to the proportion of hake in the diet are generally good, except for the high proportions indicated by the data for the proportion of *M. capensis* prey in the diet of *M. capensis* predators in the length group 50-60cm (and to a lesser extent the length groups on either side). The model estimate lies well below this data point, but still within the 95% confidence interval. The daily ration for *M. paradoxus* predators is substantially lower than that for *M. capensis* predators, but until more (ideally species-specific) information on the daily ration for Cape hake becomes available, there is no reason to consider that aspect of the results implausible. The preference functions estimated by the model are broadly consistent with the indication from the diet data that hake prefer prey that are 22-60% of predator length (see Figure 5.D.1 of Appendix 5.D), although it should be noted that the preference observed in the data is a product of predator preference (which is modelled by the preference function) and prey abundance. It is also interesting to note that the preference function estimated for *M. capensis* predators with *M. paradoxus* prey peaks at a slightly lower prey length to predator length ratio than for *M. capensis* prey, which is also consistent with the findings of Appendix 5.D.

The last Figure pertaining to the base case model is Figure 6.5n, which shows the counts of hake prey in the stomachs of hake predators by predator and prey age and species (these data are listed in Table 3.9 of Chapter 3) and the corresponding model estimates (see Equation 5.29 for how these are calculated). The fits are generally satisfactory.

Table 6.2 gives the estimates of precision for a selection of key model outputs: the pre-exploitation and 2013 spawning biomasses, the 1977, 2007 and 2013 spawning biomasses relative to pre-exploitation levels, and the reduction in the model estimate of the historical ICSEAF CPUE data between 1955 and 1977. The predation model in its current form is subject to data conflicts, a multi-modal likelihood surface, and likely also over-parameterisation (see Sections 6.4 and 6.7 and the future work Chapter 7), features which are not uncommon for many age-structured assessment models, with or without predation (S. Gaichas, *pers. comm.*), and as a result ADMB is generally not able to estimate the precision of the parameters and model outputs for the base case predation model with all its customary estimable parameters. In order to obtain the standard errors shown in Table 6.2 most of the estimable parameters (apart from the pre-exploitation biomasses, the recruitment residuals, and the ICSEAF catchability coefficients) had to be fixed at their base case values, and the model re-run with best estimates for the remaining estimable parameters from the base case as starting values for the minimisation. This approach is not ideal, but until the issues outlined above are addressed full convergence of the minimisation to the extent necessary to obtain the Hessian cannot realistically be expected. Furthermore, these confidence intervals are likely underestimates of the real uncertainty, given that they were calculated with a reduced number of estimable parameters. Nevertheless these values do indicate that the current depletion levels (B^{sp}_{2013}/K^{sp}) are not well-determined, with a 95% confidence interval that ranges roughly from 8% to

20% for *M. paradoxus* and 65% to 81% for *M. capensis*. The relative extent to which the ICSEAF CPUE is estimated to fall from 1955 to 1977 is also poorly determined.

In light of the issues outlined above, it is important to be aware that the results presented in this Chapter need to be considered in terms of their ability to qualitatively illustrate the different features of the predation model, and that the interpretations that they provide of the status of the hake resource do not yet carry nearly the same weight as those from the standard hake assessment models without explicit predation (such as in Rademeyer and Butterworth 2014b).

6.4 "Switching"

Through the countless model iterations and runs that were undertaken during the process of developing the predation model, it became clear that the model has a tendency to "switch" between fitting one group of data closely to fitting another. This can occur for a single model with different starting parameter vector values, suggesting a multi-modal negative log-likelihood surface whose global minimum does not differ greatly in log-likelihood value from subsidiary minima. An example of this is given in Figure 6.6, which shows the base case model results that have already been presented, together with the results of a re-run of the base case with different starting values for the estimable parameters. The second run achieved a better fit to the historical ICSEAF CPUE data, but a slightly lower daily ration for both *M. paradoxus* and *M. capensis* (although this latter feature does not impact the value of the negative log-likelihood). However, the spawning biomass for *M. capensis* is substantially higher for this re-run in absolute terms and further the extents of depletion for this species are much less severe than for the base case and the Rademeyer and Butterworth (2014b) models. This last feature is perhaps the major unrealistic feature of this re-run, in that such a healthy *M. capensis* stock is hardly consistent with reports of severely low catch rates in the 1970s. In terms of the total negative log-likelihood, however, there is very little difference between these two runs (-118.38 for the base case and -118.80 for the re-run). This is because what the re-run gains in its fit to the historical CPUE data, it loses elsewhere, in this case in the fit to the catch-at-length data. This of course poses a challenge to the model development process, since these two runs, while qualitatively different, are equally "good" fits to the data from a weighted negative log-likelihood point of view.

This "switching" also occurs in another form, and since this occurs in several of the sensitivity runs, some brief descriptions and terminology are given here, so as to aid discussion later. The "switching" example given above will be referred to as "Switch" Type A. A second type occurs when the model switches between medium to low values of daily ration for *M. paradoxus* with a reasonable fit to the historical ICSEAF CPUE data, to a higher daily ration for *M. paradoxus* but a poor fit to these CPUE data. For this "switch", the poor CPUE fit is the result of a much less depleted *M. paradoxus* population that exhibits oscillations of greater amplitude. This will be referred to as a "Switch" Type B. In the tabular summary below, a "✓" indicates an acceptable model estimate or fit, while a "✗" indicates one ranging between hardly and not acceptable. A "✓/✗" indicates that a "switch" only occurs in some cases for that particular category. Parentheses have been used to show in what aspects of the model fit are affected when a "switch" occurs. "Historical depletion" here refers to whether the spawning biomass trajectories are consistent with the reports of low catch-rates in the 1970s and mid 2000s and/or the historical ICSEAF CPUE data.

	Daily ration		Fit to ICSEAF	Historical depletion	
	M. paradoxus	*M. capensis*		*M. paradoxus*	*M. capensis*
"Switch" Type A	✓(✗)	✓	✓(✗)	✓	✗(✓)
"Switch" Type B	✓(✗)	✓	✗(✓)	✗(✓)	✓/✗

6.5 Sensitivity runs

Section 5.6 of Chapter 5 gave a brief outline of the sensitivities that are explored in the analyses presented in this thesis. The full details and rationales for, and discussions of these sensitivity runs are provided now.

***Sensitivity 1:* Basal mortality rate**

The base case predation model assumes an age-independent basal mortality rate of $M_s^{basal} = 0.2$ yr^{-1}. Sensitivity to this value is tested with respect to two aspects: the value of M_s^{basal}, and the assumption of age-independence. The results of these sensitivity runs are presented in Figure 6.7.

The first two of the sensitivity runs in this Figure implement values of 0.1 yr^{-1} and 0.3 yr^{-1} for M_s^{basal} (dark blue and light blue lines). The run with $M_s^{basal} = 0.1$ yr^{-1} is an example of a "Switch" Type A, as it fits to the historical ICSEAF CPUE data reasonably well, but the *M. capensis* biomass is unrealistically high with a trajectory that shows very low extent of historical depletion. Since the predation release exhibited by *M. paradoxus* is a direct consequence of the reduction of the *M. capensis* predators by the fishery, a further implication of this "Switch" Type A, and the associated low extent of depletion for *M. capensis*, is that *M. paradoxus* population does not exhibit the usual predation release for this run. The second run with $M_s^{basal} = 0.3$ yr^{-1} is an example of a "Switch" Type B, where the *M. paradoxus* daily ration is substantially higher than for the base case, but the fit to the historical ICSEAF CPUE data is poor.

The third sensitivity run shown in Figure 6.7 implements a value of 0.6 for hake aged zero, dropping linearly down to 0.2 for hake aged 2. Similarly to the $M_s^{basal} = 0.3$ yr^{-1} run, this model estimates a higher *M. paradoxus* daily ration, but exhibits a poor fit to the historical CPUE data. To summarise, increasing the basal mortality rate can help to increase the *M. paradoxus* daily ration, but at the cost of an acceptable fit to the ICSEAF CPUE data.

***Sensitivity 2:* Stock-recruitment**

This next set of sensitivities, which is shown in Figure 6.8, pertains to assumptions made about the stock-recruitment relationship, which the base case assumes to be a Beverton-Holt relationship with the steepness parameter h fixed at 0.9 (see Equation 4.8). The first sensitivity run maintains the Beverton-Holt relationship, but estimates the steepness parameter h for each species. The second sensitivity run assumes a modified Ricker formulation of the stock-recruitment relationship similar to the Rademeyer and Butterworth (2014b) model, for which the recruitment is given by:

$$R_{sym} = \left(\frac{1}{12}\right) \alpha B_{sym}^{sp} \exp(-\beta (B_{sym}^{sp})^{\gamma_R}) e^{(\zeta_{sy} - \sigma_R^2/2)} \tag{6.1}$$

where $\alpha = 12 R_{s,y_0,m_0} \exp\left(\beta (K_s^{sp})^{\gamma_R}\right)$ and $\beta = \frac{ln(5h)}{(K_s^{sp})^{\gamma_R}(1-5^{-\gamma_R})}$, and h and γ_R are estimable parameters. Similar to the Beverton-Holt Equation 4.8, the original specification for this relationship given in Rademeyer and Butterworth (2014b) has been adjusted to allow for a monthly time-step in the model.

Both these sensitivity runs achieved a better fit to the historical ICSEAF CPUE data, although this may be a consequence only of the slightly lower daily rations estimated for both *M. paradoxus* and *M. capensis*, which in turn result in a lesser extents of predation release for both species. The run that implemented the modified Ricker stock-recruitment relationship interestingly estimated a much less depleted *M. paradoxus* population, but as this feature is inconsistent with the offshore CPUE data (see Block B of Figure 6.8) and the overall negative log-likelihood for this run is substantially worse than for the base case, this run is less credible.

Stock-recruitment was identified as one of the three major axes of uncertainty during the development of the 2014 hake OMP (Rademeyer and Butterworth 2014a). For the predation model, the different forms of the stock-recruitment relationship did not yield substantially different results to the base case, but it should be noted that the theory behind these stock-recruitment relationships is based on the assumption that natural mortality rates are density-independent (i.e. constant with biomass). In such a case, if one plots the number of deaths in the population as a function of spawning biomass, this will yield a straight line that intersects with the recruitment curve at K^{sp}. For the predation model, however, the number of deaths will not have a linear relationship with biomass, since the mortality rates are density-dependent. It would be a fairly complicated exercise to ascertain the shapes of these curves and also whether the standard interpretations of the stock-recruitment parameters (such as what constitutes a biologically realistic value for h) apply in the same way for the predation model. This is discussed further under future work in Chapter 7.

***Sensitivity 3:* Increase lower limit on daily ration**

Given that the bounds for daily ration in Appendix 5.C were derived from theoretical considerations, rather than empirical data, there is still much uncertainty about what these values are in reality. The predation model tends to estimate a rather low daily ration for *M. paradoxus*, and it is of interest to ascertain how much the lower bound for daily ration could be increased before a "Switch" Type B occurs where a higher *M. paradoxus* daily rations leads to a poor fit to the ICSEAF CPUE data in particular. Note that since the daily ration tends to decrease with predator age, this lower bound is effectively the bound for the ration of the older hake predators.

Figure 6.9 shows the results for two sensitivity runs that enforced a lower limit on the daily ration of 0.2% and 0.3%. The predation model was able to implement a lower limit of 0.2%, and consequently achieve a higher *M. paradoxus* daily ration, without a "switch" occurring — the fits to the other components are very similar to the base case. Interestingly, the *M. paradoxus* biomass trajectory shows less predation release than for the base case, which in this case is likely a direct result of more *M. paradoxus* cannibalism, rather than *M. capensis* predation as has been the case previously. When the lower bound on daily ration is increased to 0.3% the model "switches", and a poor fit to the ICSEAF CPUE data results. Thus it seems that there is a limit as to how high the *M. paradoxus* daily ration (for older predators) can be pushed.

***Sensitivity 4:* Specify the daily ration of age 3 predators (to 1.53%)**

A common feature of the results that have been presented thus far is the generally different levels of daily rations that are estimated for *M. paradoxus* and *M. capensis*, with the *M. capensis* daily rations often being substantially higher than those for *M. paradoxus*. It might be argued that the two hake species should consume similar daily rations. In order to enforce this, however, some common daily ration needs to be specified, and since little is known about how the ration changes with predator size, specifying the ration for a single age group seems the best approach. Table 2.3 lists a range of daily rations as percentages of body mass from the literature. Many of the rations in this Table correspond to a relatively large range of predator lengths, but by considering

only rations reported for a smaller length range centering roughly on 30cm (which is the approximate length of hake of age 3), the average daily ration is found to be 1.53% (sd=0.8%) of body mass. While this calculation is very coarse, it at least provides some guideline for an attempt to force the *M. paradoxus* and *M. capensis* rations to be of similar magnitude.

This ration of 1.53% for age 3 predators is enforced by adding a penalty to the negative log-likelihood:

$$-lnL+ = \sum_{1999}^{2013} \sum_{s_p} (\bar{\delta}^{s_p a_p=3} - 1.53)^2/(2\sigma^2) \tag{6.2}$$

where $\bar{\delta}^{s_p a_p}$ is the model estimated daily ration for predators of age 3 (see Equation 5.31), and three different values for σ were implemented: 0.8 (corresponding to the standard deviation about the average value of 1.53%, as might be argued to be appropriate in a Bayesian prior sense), as well as smaller values of 0.4 and 0.2. The results are shown in Figure 6.10. All three runs managed to achieve a higher *M. paradoxus* daily ration, and unsurprisingly as the value of σ is decreased the difference between the *M. paradoxus* and *M. capensis* rations becomes smaller. However, all three runs also exhibit "switching", with the first two runs ($\sigma = 0.8$ and $\sigma = 0.4$) showing a "Switch" Type B with poor fits to the ICSEAF CPUE data, and the run with $\sigma = 0.2$ showing a good fit to the ICSEAF CPUE and diet data, but estimating a much higher *M. capensis* spawning biomass.

These runs suggest that while it is possible to force the two hake species to consume similar daily rations, this can be achieved only if either the *M. paradoxus* or the *M. capensis* population is less depleted than is likely given the history of the fishery.

Sensitivity 5: Reduce proportion of hake in the diet of hake predators

The calculation of the proportion of hake in the diet of hake predators from stomach content data (see Appendix 5.B) relies on several assumptions, in particular about the evacuation rate of different prey types and methods of estimating a mass-at-ingestion from the mass of partially digested prey items found in the stomach samples. Furthermore, Payne *et al.* (1987) point out that the category "unidentified fish", which have been assumed not to be hake (see Section 5.B.6 of Appendix 5.B for the reasons) could be substantially underestimated in terms of mass since most of the items that fall in this category are in an advanced state of digestion. The fact that older hake tend to evert their stomach more frequently could also lead to biases in the proportions estimated for these predators (Punt and Leslie 1995). Thus there is considerable uncertainty associated with the estimates of these proportions, which is reflected in variances that have been associated with them.

In light of these uncertainties, the next two sensitivity runs reduce the proportion of hake in the diet (and the associated variance estimates) to 67% and 50% of their original estimates. The aim is to see whether with these reductions (which are considered to be still within the bounds of reality as indicated by the diet data) could help resolve difficulties that the model experiences in estimating a higher *M. paradoxus* daily ration while maintaining a good fit to the ICSEAF CPUE data — it would seem likely that if the proportion of hake in the diet is less, then the predators (particularly the *M. paradoxus* predators) should be able to consume a higher daily ration without introducing large amplitude oscillations in the biomass trajectories.

The results are shown in Figure 6.11. The negative log-likelihood for the run where the proportions were multiplied by 2/3 (dark blue lines) is much higher than for the base case, suggesting that this may reflect a local minimum. The run where the proportion was multiplied by 1/2 clearly represents a "Switch" Type A. For both of these runs, the *M. paradoxus* population shows a smaller extent of predation release, but neither is able to simultaneously achieve a high *M. paradoxus* daily ration and a good fit to the ICSEAF CPUE data.

In conclusion, simply reducing the proportion of hake in the diet does not resolve the data conflicts for the predation model and introduce the trajectory stability as had been hoped.

***Sensitivity 6:* Force the *M. paradoxus* depletion level**

The sixth and final sensitivity set investigates how well the data determine the *M. paradoxus* depletion level. For these sensitivities, the *M. paradoxus* depletion level was forced to a series of different values by adding the following penalty to the negative log-likelihood:

$$-lnL+ = \left(\frac{B^{sp}_{par,2013}/K^{sp}_{par} - X}{2(0.02)} \right)^4 \tag{6.3}$$

where $B^{sp}_{par,2013}$ and K^{sp}_{par} are the *M. paradoxus* 2013 and pre-exploitation spawning biomasses and X is the target depletion level. The form of this penalty was chosen to ensure that the target depletion levels are matched by the model. Note that these runs were initiated at the best estimates of the parameters for the base case model.

Target depletion levels of 10% 15% 20%, 25%, 30% and 40% were considered. Figure 6.12 shows the results for a selection of these, while Table 6.3 shows the negative log-likelihoods, as well as the depletion levels that the model was able to realise, for all of these target depletion values. The results in the Figure and Table show that (a) the model is able to match all of these specified target depletion levels, (b) a higher depletion level is associated with a (slightly) greater predation release for both species (at different times) but in particular for *M. paradoxus*, and (c) the *M. paradoxus* daily ration decreases slightly as a lower extent of depletion is enforced.

The differences in the negative log-likelihoods suggest that a depletion level of roughly 15% is most likely, but only marginally so — the difference in the negative log-likelihood between depletion levels of 10% and 20% is only 0.4 log-likelihood points, suggesting that this depletion level is not very well-determined. This finding is consistent with the precision estimated for the depletion parameter, as reported in Table 6.2. Only for target depletion levels above about 30% is the deterioration in the negative log-likelihood value more marked, once again driven in part by a poorer fit to the ICSEAF CPUE data.

6.6 Projections under constant catch

A point of interest is whether taking predation and cannibalism into account explicitly leads to a different perception of the productivity of the hake resource. In order to investigate this, the model is projected into the future under the assumption of a constant annual catch[4], and the results are compared to those of the Rademeyer and Butterworth (2014b) model. There are many ways in which such projections might be undertaken, but a very simple approach was taken here whereby the Rademeyer and Butterworth (2014b) model was projected forward for three different constant catch levels (100 000t, 120 000t and 140 000t), splitting this constant catch by fleet by assuming the same proportions of catch amongst the fleets as in recent years, and then further splitting the catch into species and gender by assuming the same fishing mortality ratios as estimated in the model for the recent years. The resulting (future) catch series by species and fishing fleet was then used to project the predation model into the future. Note that in order to be comparable to the predation model, a variant of the Rademeyer and Butterworth (2014b) model was used that assumes a Beverton-Holt stock-recruitment relationship, with

[4]Constant catch, rather than constant fishing mortality, was chosen for the projections as this provided the simplest approach for an initial look at future projections.

the steepness parameter h fixed at 0.9. Appreciation is expressed to R. Rademeyer for providing the catches for these projections, as well as the biomass trajectories for the Rademeyer and Butterworth (2014b) model for comparison purposes.

The results shown in Figure 6.13 suggest that the *M. paradoxus* resource is not as productive as is estimated for the Rademeyer and Butterworth (2014b) model, since for the latter model the resource is able to sustain a higher level of future catch. An interesting feature is that under the assumption of constant catch, the predation model exhibits clear predator-prey oscillations, with a period of just over 10 years, and greater amplitudes for a higher constant catch.

The method used to obtain these projections, however, is rather simplistic, and does not have the flexibility to allow future catches to be altered in response to changing population levels. A better approach might, for example, be to assume a constant fishing mortality rate, which would automatically increase or reduce the catches if the population respectively started to increase or decline. The best way of undertaking these projections, however, would undoubtedly be to apply the hake Management Procedure to this predation model, in order to assess how the resource would behave under realistic TAC evaluation approach (see further discussion in Chapter 7).

6.7 In closing...

The results of this predation model and its variants from the sensitivity runs show that while the model is by no means up to customary single species assessment standards[5] yet, it has the ability to take hake-on-hake predation and cannibalism explicitly into account and still provide reasonable fits to the various data sources.

Both *M. paradoxus* and *M. capensis* populations exhibit (though at different times) predation release in response to a reduction of hake predators through the fishery, but not to an extent that appreciably changes the current depletion levels, which are similar to those estimated by the non-predation Rademeyer and Butterworth (2014b) model. This finding is contrary to the hope expressed by some stakeholders in the fishery that this predation release would result in an estimate of a substantially more optimistic *M. paradoxus* depletion level. When the daily ration of the *M. paradoxus* predators is increased, the *M. paradoxus* population becomes markedly less depleted, but the fits to the historical ICSEAF CPUE data then become worse. The panel for the 2015 International Stock Assessment workshop recommended that when conflict is experienced between fitting to the diet and the historical ICESAF CPUE data, higher priority should be given to the latter since the reductions in the catch-rates are an important characteristic of the South African hake fishery in the 1960s and 1970s (Dunn *et al.* 2015). This recommendation has been followed in the development of the predation model, but the question does arise as to how much confidence should be placed in the ICSEAF CPUE data, given that this series is now well over 40 years old and with the underlying detailed data that might allow a more thorough examination no longer available. Exploring different weightings for various data sources is amongst the items listed under Future work in the next Chapter.

[5]The main areas in which the standards of the predation model are below those of the single-species assessment model are: (1) there is a lack of satisfactory variance estimates for the parameters, which are essential for a defensible single-species assessment; a simpler parameterisation is likely needed in order to achieve convergence and a positive definite Hessian matrix; (2) analyses of retrospective patterns would need to be performed (a retrospective pattern is a "systematic inconsistency among a series of estimates of population size, or related assessment variables, based on increasing periods of data"; see Mohn 1999) and (3) a greater number of sensitivities would need to be explored, and more importantly the different sensitivities need to be "crossed", since the key parameter values selected for the base case predation model were inter-related, thus changing the assumptions for one sensitivity will require changes for other sensitivity assumptions in order to retain a sensible fit.

The predation model as presented in this thesis is by no means the end of the road for such an approach. The next Chapter goes into detail about various further model developments and improvements that might be investigated. One of the first and most important tasks will be to simplify the model. The extent to which the model estimates for the predation parameters in Table 6.5 vary between the different model runs indicates that the predation model as developed here is likely over-parameterised, and this will need to be addressed. During the last four years of model-development, the predation model has evolved and changed as new problem areas were uncovered, and with each iteration the understanding of the model dynamics improved. The resulting model is, however, akin to a home in which numerous building modifications have been made over the years — functional but not entirely efficient. At this point, with a model that achieves a reasonable fit to all the data sources, the equations need to be reconsidered and simplified as far as possible. Such a simplification is also important in the context of physical computing limitations, since the present predation model with its monthly time-step is at the limit what could be considered computationally practical[6]. Some thoughts on ways in which this might be achieved are given in the next Chapter.

Down the line, when the predation model has been simplified and other important modifications have been made (such as introducing non-hake predators of hake or a coastal split; see the next Chapter), it has the potential to provide valuable insights into areas of uncertainty in the current assessment model. For example, natural mortality is a major uncertainty in the standard assessment model, and the insights gained from the predation model could perhaps provide guidelines for choices for natural mortality-at-age vector values that correspond better to reality. Hence while the predation model is unlikely to reach the level of a robust stock assessment model in the immediate future, given the uncertainty around the diet-related quantities, it certainly provides a further tool to improve the assessment and management of what is South Africa's most valuable fishery.

[6] A typical run requires 24 hours, and the thesis computations and explorations were possibly only because of the availability at UCT of a high performance cluster which allowed the author to run up to 20 different variants simultaneously.

Table 6.1a: Summary table of key model outputs for ***M. paradoxus***, for the Rademeyer and Butterworth (2014b) model (referred to as "Rademeyer model"), the predation model with predation "off", the models from the base case development phase (labelled "PreBC"), for the base case (marked as BC), and for the six sets of sensitivities. The first two columns show the spawning biomasses, in thousand tons, for the pre-exploitation equilibrium (K^{sp}) and for 2013 (B^{sp}_{2013}). The next five columns show various measures of spawning biomass relative to the pre-exploitation biomass: for the years 1977 and 2007 (the two years where the fishery was experiencing severe problems with low catch rates) and for 2013 (last year considered in the model), and also the minimum and maximum spawning biomasses relative to K^{sp}, followed by the years in which they occurred in parenthesis. The last column shows the drop (from 1955 to 1977) in the model-estimated biomass index for the ICSEAF CPUE, with the difference to the relative proportion (0.28) to which the observed CPUE dropped shown in parenthesis. Note that this index reflects a combination of the two hake species (see Section 4.3.1.1). Rows shown in grey reflect notably poorer fits to the data, in terms of the criteria specified in the Table 6.3 caption.

M. paradoxus	K^{sp}	B^{sp}_{2013}	B^{sp}_{1977}/K^{sp}	B^{sp}_{2007}/K^{sp}	B^{sp}_{2013}/K^{sp}	B^{sp}_{max}/K^{sp}	B^{sp}_{min}/K^{sp}	$\hat{I}_{1977}/\hat{I}_{1955}$
Rademeyer model	1504	273	0.09	0.12	0.18	1.00 (1916)	0.09 (1977)	0.28 (0.00)
Predation "off"	1453	220	0.13	0.13	0.15	1.00 (1916)	0.12 (2006)	0.29 (-0.01)
PreBC Set 1:								
No DR constraint	563	70	0.14	0.12	0.13	1.67 (1958)	0.08 (1974)	0.27 (0.01)
DR limit	297	137	0.27	0.33	0.46	2.01 (1958)	0.16 (1973)	0.45 (-0.17)
PreBC Set 2:								
Availability	265	72	0.15	0.22	0.27	1.74 (1957)	0.09 (1974)	0.25 (0.03)
Slope DR	261	74	0.17	0.22	0.29	1.66 (1958)	0.09 (1974)	0.24 (0.04)
PreBC Set 3:								
$P_{lim} = 0.07$	265	114	0.64	0.30	0.43	1.12 (1954)	0.24 (2005)	0.38 (-0.10)
$P_{lim} = 0.05$	782	87	0.08	0.10	0.11	1.04 (1953)	0.07 (1974)	0.31 (-0.03)
PreBC Set 4:								
$P_{lim} = 0.06$ (BC)	**497**	**71**	**0.11**	**0.13**	**0.14**	**1.32 (1956)**	**0.10 (2005)**	**0.30 (-0.02)**
$P_{lim} = 0.04$	801	82	0.07	0.08	0.10	1.02 (1952)	0.04 (1974)	0.26 (0.02)
$P_{lim} = 0.03$	927	86	0.07	0.07	0.09	1.00 (1947)	0.05 (1974)	0.22 (0.06)
Sensitivity 1:								
$M^b = 0.1$	801	78	0.09	0.10	0.10	1.02 (1952)	0.07 (1974)	0.33 (-0.05)
$M^b = 0.3$	403	290	0.78	0.56	0.72	1.03 (1952)	0.46 (2005)	0.49 (-0.21)
$M^b_0 = 0.6,\ M^b_2 = 0.2$	297	148	0.99	0.39	0.50	1.16 (1956)	0.31 (2005)	0.48 (-0.20)
Sensitivity 2:								
B-H, estimate h	506	62	0.15	0.13	0.12	1.17 (1955)	0.09 (1974)	0.28 (-0.00)
Modified Ricker	506	226	0.16	0.32	0.45	1.19 (1956)	0.06 (1974)	0.31 (-0.03)
Sensitivity 3:								
$DR_{lim} = 0.2$	497	75	0.11	0.14	0.15	1.17 (1955)	0.09 (1974)	0.35 (-0.07)
$DR_{lim} = 0.3$	310	119	0.56	0.30	0.38	1.03 (1952)	0.24 (2005)	0.40 (-0.12)
Sensitivity 4:								
$\sigma_{DR(a=3)} = 0.6$	315	112	0.55	0.27	0.36	1.06 (1953)	0.22 (2005)	0.38 (-0.10)
$\sigma_{DR(a=3)} = 0.4$	304	156	0.99	0.40	0.51	1.13 (1956)	0.32 (2005)	0.51 (-0.23)
$\sigma_{DR(a=3)} = 0.2$	588	97	0.10	0.14	0.16	1.03 (1952)	0.07 (1974)	0.36 (-0.08)
Sensitivity 5:								
prop(2/3)	445	133	0.29	0.18	0.30	1.04 (1952)	0.15 (2005)	0.30 (-0.02)
prop(1/2)	594	90	0.10	0.15	0.15	1.04 (1953)	0.08 (1974)	0.35 (-0.07)
Sensitivity 6:								
10%	507	56	0.11	0.13	0.11	1.30 (1956)	0.10 (2005)	0.29 (-0.01)
15%	490	72	0.12	0.13	0.15	1.31 (1956)	0.10 (2005)	0.30 (-0.02)
20%	485	93	0.13	0.15	0.19	1.32 (1956)	0.11 (2005)	0.31 (-0.03)
25%	477	114	0.14	0.16	0.24	1.34 (1956)	0.12 (1974)	0.31 (-0.03)
30%	475	137	0.15	0.17	0.29	1.35 (1956)	0.13 (1974)	0.32 (-0.04)
40%	456	177	0.17	0.19	0.39	1.43 (1956)	0.15 (1974)	0.33 (-0.05)

Table 6.1b: Repeat of the summary Table 6.1a for ***M. capensis***. Since the ICSEAF CPUE series is species-aggregated, the last column of Table 6.1a has not been duplicated here.

M. capensis	K^{sp}	B^{sp}_{2013}	B^{sp}_{1977}/K^{sp}	B^{sp}_{2007}/K^{sp}	B^{sp}_{2013}/K^{sp}	B^{sp}_{max}/K^{sp}	B^{sp}_{min}/K^{sp}
Rademeyer model	491	373	0.38	0.49	0.76	1.00 (1916)	0.18 (1961)
Predation "off"	723	455	0.40	0.43	0.63	1.00 (1916)	0.24 (1959)
PreBC Set 1:							
No DR constraint	490	330	0.43	0.50	0.67	1.00 (1916)	0.23 (1958)
DR limit	304	251	0.62	0.58	0.83	1.00 (1916)	0.32 (1957)
PreBC Set 2:							
Availability	498	312	0.33	0.46	0.63	1.00 (1916)	0.08 (1960)
Slope DR	519	327	0.36	0.46	0.63	1.00 (1916)	0.08 (1959)
PreBC Set 3:							
$P_{lim} = 0.07$	572	325	0.27	0.46	0.57	1.00 (1916)	0.06 (1960)
$P_{lim} = 0.05$	1259	929	0.70	0.58	0.74	1.00 (1916)	0.57 (2008)
PreBC Set 4:							
$P_{lim} = 0.06$ (BC)	**280**	**204**	**0.56**	**0.47**	**0.73**	**1.00 (1916)**	**0.19 (1957)**
$P_{lim} = 0.04$	650	379	0.35	0.45	0.58	1.00 (1916)	0.16 (1959)
$P_{lim} = 0.03$	756	371	0.26	0.37	0.49	1.00 (1916)	0.11 (1960)
Sensitivity 1:							
$M^b = 0.1$	3024	1987	0.67	0.68	0.66	1.00 (1916)	0.64 (2011)
$M^b = 0.3$	326	234	0.43	0.43	0.72	1.00 (1916)	0.13 (1957)
$M^b_0 = 0.6,\ M^b_2 = 0.2$	527	323	0.35	0.45	0.61	1.00 (1916)	0.08 (1959)
Sensitivity 2:							
B-H, estimate h	461	245	0.29	0.38	0.53	1.00 (1916)	0.25 (1957)
Modified Ricker	461	303	0.28	0.44	0.66	1.00 (1916)	0.25 (1957)
Sensitivity 3:							
$DR_{lim} = 0.2$	284	215	0.59	0.51	0.76	1.00 (1916)	0.23 (1957)
$DR_{lim} = 0.3$	476	288	0.36	0.48	0.61	1.00 (1916)	0.08 (1958)
Sensitivity 4:							
$\sigma_{DR(a=3)} = 0.6$	637	376	0.29	0.48	0.59	1.00 (1916)	0.06 (1960)
$\sigma_{DR(a=3)} = 0.4$	542	329	0.33	0.44	0.61	1.00 (1916)	0.07 (1959)
$\sigma_{DR(a=3)} = 0.2$	1422	1117	0.74	0.60	0.79	1.00 (1916)	0.60 (2008)
Sensitivity 5:							
prop(2/3)	545	307	0.30	0.51	0.56	1.00 (1916)	0.07 (1960)
prop(1/2)	1410	1078	0.69	0.59	0.76	1.00 (1916)	0.59 (2008)
Sensitivity 6:							
10%	285	206	0.55	0.48	0.72	1.00 (1916)	0.18 (1957)
15%	285	209	0.73	0.56	0.48	1.00 (1916)	0.18 (1957)
20%	285	211	0.56	0.48	0.74	1.00 (1916)	0.18 (1957)
25%	283	213	0.75	0.56	0.48	1.00 (1916)	0.19 (1957)
30%	282	214	0.56	0.47	0.76	1.00 (1916)	0.18 (1957)
40%	267	211	0.57	0.46	0.79	1.00 (1916)	0.19 (1957)
10%	285	206	0.72	0.55	0.48	1.00 (1916)	0.18 (1957)

Table 6.2: Key model outputs from Tables 6.1a and 6.1b are repeated here with their standard errors shown in parenthesis. Note that because of the basis used to calculate these standard errors (see Section 6.3 for details), they are negatively biased to extents that are unknown.

	M. paradoxus		*M. capensis*	
K^{sp}	497	(1)	280	(3)
B^{sp}_{2013}	71	(13)	205	(10)
B^{sp}_{1977}/K^{sp}	0.11	(0.02)	0.56	(0.03)
B^{sp}_{2007}/K^{sp}	0.13	(0.02)	0.48	(0.02)
B^{sp}_{2013}/K^{sp}	0.14	(0.03)	0.73	(0.04)
$\hat{I}_{1977}/\hat{I}_{1955}$	0.30	(0.06)	-	-

Table 6.3: Negative log-likelihood components for the models from the base case development phase (labelled "PreBC"), for the base case (marked as BC), and for the six sets of sensitivities. The first two columns list the total negative log-likelihoods with and without penalties, and the following three columns give the break-down of the negative log-likelihood into the non-predation and predation-related components, as well as the penalties (see Section 6.1). The negative log-likelihood components for the CPUE, catch-at-length and diet-related data are also listed. "Prop cc", "Prop cp" and "Prop pp" denote the proportions of hake in the diet of hake for the three *M. capensis* and *M. paradoxus* pairings. For Sensitivity 6, the *M. paradoxus* depletion levels that were realised by the model have been included. Rows are shown in grey if the total negative log-likelihood without penalties is greater than -110 or if the ICSEAF component is greater than -20, thus reflecting notably poorer fits to the data.

Run	**Total -lnL**		**-lnL components**			**CPUE**			**Catch-at-length**		**Diet components**			
	Total	w/o penalties	Non-predation	Predation	Penalties	Offshore	ICSEAF	Survey	Commercial	Survey	Preference	Prop cc	Prop cp	Prop pp
Predation "off"	-230.94	-260.94	-260.94	0.00	29.99	-179.02	-39.36	-31.13	-62.17	50.74	0.00	0.00	0.00	0.00
PreBC Set 1:														
No DR constraint	-112.86	-128.81	-248.57	119.76	15.94	-174.49	-36.05	-31.64	-56.28	49.89	40.05	19.59	46.12	14.00
DR limit	-101.87	-116.68	-238.48	121.81	14.80	-172.53	-28.60	-30.44	-57.34	50.43	40.37	16.68	46.55	18.20
PreBC Set 2:														
Availability	-125.03	-141.49	-250.59	109.10	16.47	-178.80	-39.60	-31.98	-51.80	51.57	40.37	7.82	44.94	15.98
Slope DR	-116.93	-135.01	-245.48	110.47	18.08	-176.42	-38.47	-31.54	-50.43	51.37	40.77	6.90	44.90	17.91
PreBC Set 3:														
$P_{lim} = 0.07$	-104.21	-119.26	-230.03	110.77	15.05	-172.36	-13.22	-31.06	-62.80	49.41	38.54	6.50	48.27	17.46
$P_{lim} = 0.05$	-123.19	-138.65	-244.01	105.36	15.46	-180.81	-39.47	-31.27	-41.05	48.58	40.58	6.92	43.75	14.11
PreBC Set 4:														
$P_{lim} = 0.06$ (BC)	**-118.38**	**-134.33**	**-242.65**	**108.32**	**15.95**	**-179.37**	**-32.44**	**-31.27**	**-49.71**	**50.14**	**40.09**	**8.08**	**45.88**	**14.27**
$P_{lim} = 0.04$	-120.91	-136.32	-243.42	107.10	15.41	-174.34	-37.71	-30.99	-50.65	50.26	41.01	7.15	44.82	14.13
$P_{lim} = 0.03$	-111.62	-129.90	-241.78	111.88	18.28	-172.75	-38.28	-30.68	-51.04	50.96	44.83	8.07	44.77	14.21
Sensitivity 1:														
$M^b = 0.1$	-115.24	-132.36	-239.42	107.06	17.12	-189.53	-38.13	-33.00	-27.84	49.08	42.87	7.29	45.31	11.59
$M^b = 0.3$	-80.51	-97.20	-221.74	124.54	16.68	-167.83	-15.39	-29.31	-58.58	49.38	38.87	6.94	58.88	19.85
$M_0^b = 0.6,\ M_2^b = 0.2$	-83.63	-98.41	-225.70	127.29	14.78	-169.84	-12.79	-31.09	-60.42	48.45	54.22	6.61	49.77	16.69
Sensitivity 2:														
B-H, estimate h	-123.00	-138.14	-246.11	107.97	15.15	-174.93	-37.88	-30.85	-51.75	49.30	40.46	7.08	45.84	14.59
Modified Ricker	-109.79	-127.94	-241.09	113.15	18.15	-168.66	-38.27	-31.02	-51.47	48.34	40.82	9.46	46.98	15.89
Sensitivity 3:														
$DR_{lim} = 0.2$	-116.07	-131.47	-239.42	107.95	15.40	-178.80	-32.40	-30.94	-46.45	49.17	40.11	7.79	45.53	14.52
$DR_{lim} = 0.3$	-91.91	-108.37	-224.66	116.30	16.46	-172.94	-12.44	-29.66	-57.42	47.80	40.55	6.50	49.01	20.24
Sensitivity 4:														
$\sigma_{DR(a=3)} = 0.6$	-98.84	-115.70	-227.08	111.38	16.86	-171.41	-13.34	-29.26	-62.63	49.55	39.09	7.31	48.46	16.53
$\sigma_{DR(a=3)} = 0.4$	-90.04	-105.40	-227.17	121.77	15.36	-169.89	-13.55	-31.20	-60.69	48.16	52.17	6.58	46.52	16.50
$\sigma_{DR(a=3)} = 0.2$	-116.18	-132.26	-238.80	106.54	16.08	-182.88	-37.46	-31.23	-34.89	47.67	39.38	6.82	45.85	14.48
Sensitivity 5:														
prop(2/3)	-85.20	-98.46	-223.12	124.65	13.26	-167.63	-16.97	-32.45	-55.36	49.30	41.76	6.60	51.40	24.89
prop(1/2)	-109.59	-124.94	-239.97	115.03	15.35	-182.90	-38.16	-32.42	-34.56	48.08	39.63	7.21	45.07	23.13
Sensitivity 6:														
10% (realised 11%)	-117.44	-133.54	-241.99	108.45	16.10	-179.20	-32.57	-31.04	-49.43	50.25	40.20	8.04	46.23	13.98
15% (realised 15%)	-118.16	-134.46	-242.67	108.22	16.30	-179.43	-32.38	-31.36	-49.63	50.12	40.06	8.00	45.90	14.26
20% (realised 19%)	-117.81	-134.45	-243.53	109.08	16.64	-178.28	-32.19	-31.24	-51.56	49.74	40.09	8.04	46.23	14.71
25% (realised 24%)	-116.55	-133.67	-243.72	110.05	17.12	-177.22	-31.94	-31.21	-52.88	49.53	40.17	8.12	46.56	15.20
30% (realised 29%)	-114.95	-132.55	-243.54	111.00	17.60	-175.99	-31.62	-31.07	-54.13	49.27	40.23	8.39	46.84	15.53
40% (realised 39%)	-110.36	-129.23	-242.12	112.88	18.87	-174.34	-30.74	-30.77	-55.55	49.28	40.42	8.69	47.51	16.26

Table 6.4: Parameter estimates for the non-predation components of the model. See Table 4.7 for the parameter bounds. Values in grey indicate that the parameter in question was fixed for that model run.

Parameter	h		γ^R		q^{ICSEAF}			r^{ICSEAF}	γ^{ICSEAF}	σ^{GLM}				σ^{ICSEAF}	
	par	cap	par	cap	z1(cap)	z2(cap)	z2(par)			WC(par)	WC(cap)	SC(par)	SC(cap)	WC	SC
PreBC Set 1:															
No DR constraint	0.90	0.90	-	-	0.009	0.326	0.002	9.74	0.000	0.20	0.15	0.27	0.15	0.25	0.25
DR limit	0.90	0.90	-	-	0.015	0.002	0.003	10.84	0.367	0.21	0.15	0.26	0.15	0.25	0.41
PreBC Set 2:															
Availability	0.90	0.90	-	-	0.018	0.187	0.003	10.89	0.001	0.19	0.15	0.25	0.15	0.25	0.25
Slope DR	0.90	0.90	-	-	0.017	0.001	0.003	10.53	0.000	0.20	0.15	0.25	0.15	0.25	0.25
PreBC Set 3:															
$P_{lim} = 0.07$	0.90	0.90	-	-	0.016	0.020	0.002	15.98	0.309	0.21	0.15	0.25	0.17	0.37	0.51
$P_{lim} = 0.05$	0.90	0.90	-	-	0.003	0.019	0.002	9.15	0.009	0.20	0.15	0.25	0.15	0.25	0.25
PreBC Set 4:															
$P_{lim} = 0.04$	0.90	0.90	-	-	0.013	0.000	0.002	10.17	0.150	0.20	0.15	0.26	0.15	0.25	0.25
$P_{lim} = 0.03$	0.90	0.90	-	-	0.008	0.063	0.002	11.53	0.002	0.19	0.15	0.26	0.16	0.25	0.25
Sensitivity 1:															
$M^b = 0.1$	0.90	0.90	-	-	0.003	0.094	0.002	8.93	0.001	0.15	0.15	0.25	0.15	0.25	0.25
$M^b = 0.3$	0.90	0.90	-	-	0.011	0.281	0.001	17.58	0.017	0.16	0.15	0.25	0.25	0.34	0.49
$M_0^b = 0.6,\ M_2^b = 0.2$	0.90	0.90	-	-	0.014	0.323	0.001	15.69	0.005	0.19	0.15	0.24	0.22	0.36	0.57
Sensitivity 2:															
B-H, estimate h	0.72	0.95	-	-	0.010	0.063	0.002	10.14	0.006	0.20	0.15	0.28	0.15	0.25	0.25
Modified Ricker	0.92	0.54	0.41	0.01	0.006	0.133	0.002	11.22	0.011	0.24	0.15	0.28	0.15	0.25	0.25
Sensitivity 3:															
$DR_{lim} = 0.2$	0.90	0.90	-	-	0.015	0.006	0.003	9.71	0.001	0.21	0.15	0.25	0.15	0.25	0.34
$DR_{lim} = 0.3$	0.90	0.90	-	-	0.017	0.026	0.002	14.88	0.253	0.21	0.15	0.25	0.17	0.35	0.61
Sensitivity 4:															
$\sigma_{DR(a=3)} = 0.6$	0.90	0.90	-	-	0.011	1.572	0.002	15.05	0.004	0.21	0.15	0.25	0.18	0.34	0.60
$\sigma_{DR(a=3)} = 0.4$	0.90	0.90	-	-	0.020	0.014	0.001	15.55	0.437	0.19	0.15	0.24	0.22	0.34	0.59
$\sigma_{DR(a=3)} = 0.2$	0.90	0.90	-	-	0.003	1.264	0.003	8.60	0.000	0.19	0.15	0.25	0.15	0.25	0.27
Sensitivity 5:															
prop(2/3)	0.90	0.90	-	-	0.170	0.005	0.001	16.54	0.939	0.24	0.15	0.26	0.15	0.43	0.25
prop(1/2)	0.90	0.90	-	-	0.003	0.004	0.002	9.34	0.158	0.19	0.15	0.25	0.15	0.25	0.25
Sensitivity 6:															
10%	0.90	0.90	-	-	0.017	0.001	0.003	9.64	0.028	0.21	0.15	0.25	0.15	0.25	0.32
20%	0.90	0.90	-	-	0.022	0.003	0.002	10.06	0.263	0.21	0.15	0.25	0.15	0.25	0.34
30%	0.90	0.90	-	-	0.017	0.012	0.002	10.44	0.057	0.20	0.15	0.25	0.15	0.25	0.36
40%	0.90	0.90	-	-	0.016	0.017	0.002	10.76	0.038	0.20	0.15	0.25	0.15	0.25	0.37

Table 6.5: Parameter estimates for the predation components of the model. See Table 5.1 for details of the parameters, their bounds and cross-references to the relevant equations where they are first used.

Parameter	ν			$ln(\nu_{other})^*$		$\tilde{\nu}$			$ln(\tilde{\nu}_{other})^*$		α			$\tilde{G}$		ω		$\tilde{\omega}$		o		$ln(\tilde{o})^*$		s_D
Species	cc	cp	pp	cap	par	cc	cp	pp	cap	par	cap	par	cc	cp	pp	cap	par	cap	par	cap	par	cap	par	cap
PreBC Set 1:																								
No DR constraint	0.777	0.915	0.031	-28.66	-22.20	1.097	4.930	0.348	1.20	7.43	14.9	17.9	0.81	0.90	0.94	13.98	13.32	2.48	5.53	0.29	0.97	33.42	27.48	0.00
DR limit	7.725	8.626	0.045	-37.37	-39.22	34.154	0.508	0.000	4.14	6.11	13.3	20.6	0.76	0.88	0.96	5.80	19.97	0.02	0.00	0.31	0.87	44.89	45.00	0.00
PreBC Set 2:																								
Availability	7.440	6.587	0.101	1.38	-39.75	47.823	0.053	0.442	0.01	7.26	16.1	17.6	0.83	0.93	0.97	17.81	0.04	3.31	0.25	0.21	0.93	6.73	48.33	0.04
Slope DR	8.161	7.004	0.068	-23.44	-39.96	43.917	0.420	0.000	0.73	9.11	16.2	16.3	0.83	0.94	0.96	19.76	1.51	2.98	3.25	0.17	0.84	28.83	45.05	0.05
PreBC Set 3:																								
$P_{lim} = 0.07$	14.163	10.446	0.690	-34.22	-20.58	58.842	0.000	6.514	0.01	8.53	15.3	22.9	0.82	0.93	0.99	19.28	18.13	2.86	3.81	0.16	0.93	39.87	28.94	0.09
$P_{lim} = 0.05$	4.893	6.318	1.283	-20.75	-28.52	12.104	3.872	14.858	0.03	8.98	14.8	15.8	0.83	0.92	0.95	0.49	0.00	0.53	0.88	0.17	0.94	26.28	37.67	0.09
PreBC Set 4:																								
$P_{lim} = 0.06$ (BC)	2.867	2.643	2.899	-33.64	-39.66	8.844	0.768	41.619	2.37	10.26	16.8	17.3	0.79	0.92	0.95	17.87	17.06	1.34	3.16	0.26	1.04	39.20	50.00	0.03
$P_{lim} = 0.04$	1.229	1.019	0.221	-36.88	-28.31	1.484	4.389	0.184	1.47	6.18	15.3	14.8	0.85	0.95	0.95	13.10	19.95	3.52	2.88	0.14	0.96	40.00	35.30	0.07
$P_{lim} = 0.03$	1.503	1.155	0.275	-36.84	-16.60	0.779	11.183	0.002	1.45	4.90	16.0	9.9	0.91	0.96	0.89	15.92	10.78	4.41	0.04	0.11	0.93	39.73	23.54	0.07
Sensitivity 1:																								
$M^b = 0.1$	12.707	18.066	11.448	-39.99	-30.45	4.084	9.397	74.544	0.03	10.93	13.0	13.1	0.87	0.90	0.94	0.01	0.00	0.58	0.95	0.15	0.98	46.42	42.00	0.10
$M^b = 0.3$	5.486	2.207	0.082	-3.40	-19.14	31.900	0.045	0.004	1.63	7.52	15.6	11.6	0.81	0.92	0.86	17.79	17.37	0.03	2.93	0.32	1.11	9.96	27.57	0.08
$M_0^b = 0.6,\ M_2^b = 0.2$	20.000	12.609	4.779	2.07	-34.04	79.866	0.000	55.754	0.06	9.77	15.4	4.5	0.79	0.91	0.58	20.00	20.00	2.29	1.48	0.18	0.93	6.57	46.80	0.08
Sensitivity 2:																								
B-H, estimate h	2.625	2.287	2.149	-31.64	-39.89	0.050	9.668	26.830	0.97	9.56	14.8	16.1	0.80	0.92	0.92	13.86	0.05	1.43	0.80	0.21	0.97	36.46	49.51	0.05
Modified Ricker	0.789	0.421	4.423	2.71	7.34	9.412	13.911	21.669	0.23	0.96	0.8	0.9	0.99	-19.98	-15.13	4.01	0.41	1.06	1.15	0.10	0.10	0.03	-0.40	1.38
Sensitivity 3:																								
$DR_{lim} = 0.2$	2.752	2.497	1.428	-28.49	-27.37	8.032	0.046	11.017	3.02	9.08	16.6	19.7	0.79	0.91	0.97	19.80	11.24	2.28	2.74	0.26	1.02	33.99	37.01	0.04
$DR_{lim} = 0.3$	5.226	3.207	1.821	-37.60	-39.67	0.551	15.881	9.346	0.27	8.46	15.3	15.2	0.81	0.94	0.90	0.00	0.01	0.46	0.18	0.15	1.02	42.29	49.76	0.08
Sensitivity 4:																								
$\sigma_{DR(a=3)} = 0.6$	1.607	1.118	0.920	-15.80	-39.58	2.298	4.681	6.550	0.55	8.10	15.6	18.5	0.84	0.94	0.95	3.95	17.51	1.29	3.09	0.14	0.91	19.08	48.05	0.08
$\sigma_{DR(a=3)} = 0.4$	16.770	10.616	0.733	1.97	-39.24	73.445	0.001	7.452	0.15	7.78	15.2	4.2	0.81	0.94	0.58	13.34	17.02	2.07	1.44	0.16	0.91	6.32	49.99	0.08
$\sigma_{DR(a=3)} = 0.2$	11.285	15.422	1.650	-35.59	-19.27	25.517	9.450	16.909	0.02	9.56	15.4	19.2	0.80	0.91	0.95	19.39	19.89	1.61	3.69	0.20	1.04	42.55	29.54	0.08
Sensitivity 5:																								
prop(2/3)	10.154	7.234	5.304	9.51	6.76	38.192	0.093	15.176	0.09	7.33	16.3	30.7	0.80	0.93	1.02	18.59	0.33	2.57	0.39	0.16	0.72	6.00	12.79	0.09
prop(1/2)	13.131	18.362	2.772	-12.89	-34.98	21.044	16.755	52.916	0.39	9.13	14.9	18.1	0.81	0.91	0.96	0.00	0.13	0.34	0.25	0.17	0.77	20.70	45.35	0.08
Sensitivity 6:																								
10%	5.157	4.687	5.474	-32.99	-37.99	16.366	2.176	78.076	3.34	10.89	17.2	19.4	0.79	0.92	0.97	19.01	19.96	2.04	3.91	0.26	1.03	39.05	48.89	0.03
20%	5.972	5.337	3.279	-20.31	-38.76	19.367	1.448	48.195	3.66	10.25	16.6	17.6	0.79	0.92	0.95	20.00	18.82	2.30	3.49	0.26	0.99	26.51	49.07	0.04
30%	4.819	4.261	6.225	-34.66	-38.36	15.644	1.170	95.882	3.38	10.66	16.5	16.6	0.79	0.91	0.94	17.48	19.70	1.99	3.23	0.26	0.96	40.67	49.19	0.04
40%	3.067	2.644	5.569	-36.67	-39.03	8.831	0.846	91.368	2.14	10.43	16.0	16.3	0.79	0.91	0.94	19.63	20.00	1.21	2.98	0.25	0.93	42.23	49.68	0.04

*Parameter is estimated in log-space.

Table 6.6a: Breakdown of the hake prey consumed by hake predators, by predator and prey species and age. The total number of hake of a given prey age that were consumed by hake predators is given in the left column. The main table lists the percentage of that total that was consumed by hake predators of a given age. These results are for the base case model and the year **1916** (i.e. pre-exploitation equilibrium).

		Total no.	Predator age														
		consumed	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
M. capensis predators, *M. capensis* prey																	
Prey age	0	1484503.51	35.62	41.64	17.40	4.29	0.85	0.16	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	1	637293.60	-	8.06	32.97	33.06	16.71	6.05	2.00	0.70	0.26	0.11	0.04	0.02	0.01	0.00	0.01
	2	184447.07	-	-	1.08	14.45	28.41	24.51	14.79	7.99	4.22	2.19	1.10	0.54	0.26	0.12	0.33
	3	60864.86	-	-	-	0.13	3.88	13.39	19.16	18.66	15.12	10.82	7.01	4.21	2.40	1.32	3.92
	4	27266.95	-	-	-	-	0.01	0.75	4.34	10.01	14.55	15.89	14.16	10.91	7.60	4.93	16.83
	5	13083.33	-	-	-	-	-	0.00	0.15	1.38	4.74	9.25	12.53	13.25	11.81	9.35	37.55
	6	5725.36	-	-	-	-	-	-	0.00	0.04	0.54	2.48	5.99	9.59	11.70	11.83	57.83
	7	2166.67	-	-	-	-	-	-	-	0.00	0.02	0.29	1.62	4.61	8.51	11.75	73.21
	8	683.27	-	-	-	-	-	-	-	-	0.00	0.01	0.22	1.45	4.73	9.86	83.74
	9	163.19	-	-	-	-	-	-	-	-	-	0.00	0.01	0.25	1.92	7.09	90.73
	10	25.32	-	-	-	-	-	-	-	-	-	-	0.00	0.02	0.49	4.21	95.29
	11	2.10	-	-	-	-	-	-	-	-	-	-	-	0.00	0.05	1.86	98.09
	12	0.07	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.46	99.53
	13	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	99.97
	14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100.00
M. capensis predators, *M. paradoxus* prey																	
Prey age	0	3272375.46	20.57	35.13	26.38	11.93	4.08	1.26	0.40	0.15	0.06	0.03	0.01	0.01	0.00	0.00	0.00
	1	1380562.87	-	1.75	15.93	28.14	24.03	14.12	7.28	3.81	2.09	1.18	0.66	0.37	0.20	0.11	0.34
	2	474660.95	-	-	0.08	3.03	11.58	17.19	16.72	13.88	10.84	8.04	5.64	3.77	2.43	1.53	5.25
	3	201210.09	-	-	-	0.00	0.33	2.41	6.13	9.72	12.11	12.76	11.78	9.82	7.60	5.58	21.76
	4	85437.80	-	-	-	-	0.00	0.03	0.45	1.92	4.62	7.80	10.25	11.25	10.85	9.54	43.29
	5	29162.10	-	-	-	-	-	0.00	0.00	0.11	0.74	2.46	5.20	8.14	10.35	11.35	61.65
	6	7501.92	-	-	-	-	-	-	0.00	0.00	0.04	0.40	1.66	4.20	7.65	11.07	74.99
	7	1647.40	-	-	-	-	-	-	-	0.00	0.00	0.02	0.30	1.52	4.52	9.40	84.23
	8	324.97	-	-	-	-	-	-	-	-	0.00	0.00	0.02	0.34	2.05	7.00	90.58
	9	45.53	-	-	-	-	-	-	-	-	-	0.00	0.00	0.03	0.63	4.43	94.90
	10	3.60	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.10	2.18	97.72
	11	0.12	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.68	99.32
	12	0.00	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.07	99.93
	13	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	100.00
	14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100.00
M. paradoxus predators, *M. paradoxus* prey																	
Prey age	0	561818.03	6.19	20.48	29.95	23.13	12.27	4.98	1.82	0.71	0.28	0.11	0.04	0.02	0.01	0.00	0.01
	1	709340.41	-	0.34	6.18	19.15	26.08	20.74	12.51	7.18	3.86	1.95	0.95	0.46	0.22	0.11	0.28
	2	389916.23	-	-	0.02	1.35	8.16	16.51	18.98	17.51	13.52	9.12	5.62	3.27	1.85	1.02	3.07
	3	163745.01	-	-	-	0.00	0.26	2.47	7.31	12.88	15.91	15.34	12.52	9.16	6.23	4.03	13.91
	4	60580.24	-	-	-	-	0.00	0.05	0.68	3.08	7.25	11.15	12.96	12.51	10.64	8.29	33.39
	5	18872.29	-	-	-	-	-	0.00	0.01	0.23	1.39	4.05	7.49	10.26	11.49	11.16	53.93
	6	4687.07	-	-	-	-	-	-	0.00	0.00	0.10	0.76	2.65	5.76	9.12	11.63	69.98
	7	1033.01	-	-	-	-	-	-	-	0.00	0.00	0.06	0.55	2.28	5.71	10.29	81.10
	8	211.79	-	-	-	-	-	-	-	-	0.00	0.00	0.06	0.59	2.80	7.97	88.58
	9	32.35	-	-	-	-	-	-	-	-	-	0.00	0.00	0.08	1.00	5.34	93.58
	10	3.02	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.21	2.94	96.84
	11	0.14	-	-	-	-	-	-	-	-	-	-	-	0.00	0.02	1.17	98.81
	12	0.00	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.25	99.75
	13	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	99.99
	14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100.00

Table 6.6b: Repeat of Table 6.6a for the base case model and the year **2013** (i.e. the last year considered in the model).

		Total no. consumed	Predator age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
M. capensis predators, *M. capensis* prey																	
Prey age	0	1506453.20	36.69	42.61	16.33	3.49	0.65	0.17	0.05	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	1	597889.45	-	9.20	34.51	30.00	14.34	6.97	3.11	1.22	0.47	0.13	0.04	0.01	0.00	0.00	0.00
	2	198615.29	-	-	0.97	11.35	21.09	24.41	19.88	12.02	6.54	2.32	0.81	0.32	0.13	0.06	0.10
	3	69487.49	-	-	-	0.09	2.49	11.52	22.25	24.25	20.24	9.93	4.47	2.14	1.04	0.56	1.01
	4	20990.77	-	-	-	-	0.01	0.83	6.53	16.86	25.27	18.92	11.71	7.20	4.28	2.73	5.64
	5	6243.71	-	-	-	-	-	0.00	0.34	3.56	12.59	16.86	15.86	13.38	10.20	7.93	19.27
	6	2661.21	-	-	-	-	-	-	0.00	0.14	1.96	6.14	10.34	13.25	13.84	13.75	40.58
	7	1136.79	-	-	-	-	-	-	-	0.00	0.07	0.83	3.29	7.49	11.83	16.05	60.44
	8	359.65	-	-	-	-	-	-	-	-	0.00	0.03	0.48	2.55	7.15	14.63	75.16
	9	81.98	-	-	-	-	-	-	-	-	-	0.00	0.02	0.46	3.04	11.02	85.45
	10	8.24	-	-	-	-	-	-	-	-	-	-	0.00	0.03	0.79	6.72	92.46
	11	0.45	-	-	-	-	-	-	-	-	-	-	-	0.00	0.09	3.02	96.89
	12	0.01	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.76	99.23
	13	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05	99.95
	14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100.00
M. capensis predators, *M. paradoxus* prey																	
Prey age	0	2750224.01	21.84	37.08	25.54	10.01	3.24	1.34	0.58	0.23	0.10	0.03	0.01	0.00	0.00	0.00	0.00
	1	1078650.87	-	1.90	15.84	24.26	19.58	15.42	10.73	6.28	3.56	1.37	0.53	0.24	0.11	0.06	0.11
	2	379786.61	-	-	0.07	2.23	8.05	16.02	21.04	19.54	15.73	8.01	3.90	2.08	1.15	0.71	1.47
	3	94805.38	-	-	-	0.00	0.29	2.81	9.66	17.15	21.97	15.85	10.17	6.77	4.48	3.23	7.62
	4	17251.27	-	-	-	-	0.00	0.06	1.08	5.17	12.74	14.61	13.41	11.77	9.73	8.41	23.02
	5	4677.58	-	-	-	-	-	0.00	0.02	0.41	2.77	6.14	9.12	11.45	12.51	13.49	44.10
	6	1078.86	-	-	-	-	-	-	0.00	0.00	0.18	1.15	3.38	6.87	10.74	15.28	62.38
	7	217.06	-	-	-	-	-	-	-	0.00	0.00	0.08	0.66	2.69	6.86	14.03	75.68
	8	26.85	-	-	-	-	-	-	-	-	0.00	0.00	0.05	0.63	3.25	10.92	85.14
	9	1.74	-	-	-	-	-	-	-	-	-	0.00	0.00	0.06	1.03	7.10	91.81
	10	0.04	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.16	3.54	96.30
	11	0.00	-	-	-	-	-	-	-	-	-	-	-	0.00	0.01	1.10	98.89
	12	0.00	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.12	99.88
	13	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	100.00
	14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100.00
M. paradoxus predators, *M. paradoxus* prey																	
Prey age	0	251804.13	9.69	28.20	30.98	15.78	9.12	4.05	1.61	0.46	0.09	0.01	0.00	0.00	0.00	0.00	0.00
	1	222376.01	-	0.63	8.73	17.81	26.40	22.99	15.10	6.27	1.74	0.29	0.03	0.00	0.00	0.00	0.00
	2	78728.60	-	-	0.04	1.70	11.20	24.83	31.11	20.75	8.28	1.85	0.22	0.02	0.00	0.00	0.00
	3	10932.40	-	-	-	0.01	0.80	8.30	26.86	34.15	21.73	6.91	1.08	0.15	0.02	0.00	0.00
	4	716.88	-	-	-	-	0.00	0.60	9.28	30.39	36.54	18.27	4.02	0.75	0.14	0.02	0.01
	5	45.60	-	-	-	-	-	0.00	0.77	11.93	36.86	34.54	11.83	3.15	0.76	0.11	0.05
	6	1.90	-	-	-	-	-	-	0.00	1.12	16.52	40.14	26.30	11.04	3.76	0.71	0.39
	7	0.07	-	-	-	-	-	-	-	0.00	1.69	19.43	32.56	25.93	13.98	3.72	2.69
	8	0.00	-	-	-	-	-	-	-	-	0.01	1.78	14.31	29.14	29.66	12.51	12.59
	9	0.00	-	-	-	-	-	-	-	-	-	0.01	1.15	11.06	28.92	23.14	35.72
	10	0.00	-	-	-	-	-	-	-	-	-	-	0.00	0.90	11.20	23.41	64.48
	11	0.00	-	-	-	-	-	-	-	-	-	-	-	0.00	1.27	12.96	85.76
	12	0.00	-	-	-	-	-	-	-	-	-	-	-	-	0.01	2.99	97.00
	13	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.13	99.87
	14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100.00

Table 6.7a: Daily per capita consumption of hake prey (by prey numbers) by hake predators **for the year 1916** (i.e. pre-exploitation equilibrium) for the base case. This per capita consumption has been calculated as $\sum_m \left(E^{s_p a_p}_{saym} / (N^{s_p a_p}_{ym} \gamma^{s_p a_p}_{sa})\right) /365$, where $E^{s_p a_p}_{saym}$ is the number of hake prey of species s and age a consumed by hake predators of species s_p and age a_p in month m of year y (Equation 5.5); $N^{s_p a_p}_{ym}$ is the number of hake predators of species s_p and age a_p in month m of year y, and $\gamma^{s_p a_p}_{sa}$ is the preference that a hake predator of species s_p and age a_p exhibits for a hake prey of species s and age a.

		Predator age														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
M. capensis predators, *M. capensis* prey																
Prey age	0	0.00	0.02	0.04	0.08	0.13	0.20	0.29	0.40	0.52	0.65	0.80	0.94	1.10	1.25	1.40
	1	-	0.01	0.02	0.03	0.05	0.08	0.12	0.16	0.21	0.26	0.32	0.38	0.44	0.50	0.56
	2	-	-	0.01	0.01	0.02	0.03	0.05	0.06	0.08	0.10	0.13	0.15	0.18	0.20	0.22
	3	-	-	-	0.01	0.01	0.01	0.02	0.03	0.04	0.05	0.05	0.07	0.08	0.09	0.10
	4	-	-	-	-	0.00	0.01	0.01	0.01	0.02	0.02	0.03	0.03	0.04	0.04	0.05
	5	-	-	-	-	-	0.00	0.00	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02
	6	-	-	-	-	-	-	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01
	7	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01
	8	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	9	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00
	10	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00
	11	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
	12	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00
	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00
M. capensis predators, *M. paradoxus* prey																
Prey age	0	0.01	0.03	0.07	0.15	0.28	0.47	0.73	1.07	1.49	2.01	2.63	3.35	4.18	5.13	6.20
	1	-	0.01	0.03	0.06	0.11	0.19	0.29	0.42	0.59	0.80	1.05	1.33	1.67	2.04	2.47
	2	-	-	0.01	0.02	0.04	0.07	0.12	0.17	0.24	0.32	0.42	0.53	0.66	0.81	0.98
	3	-	-	-	0.01	0.02	0.03	0.05	0.07	0.09	0.13	0.17	0.21	0.26	0.32	0.39
	4	-	-	-	-	0.01	0.01	0.02	0.03	0.04	0.05	0.07	0.08	0.11	0.13	0.16
	5	-	-	-	-	-	0.00	0.01	0.01	0.01	0.02	0.03	0.03	0.04	0.05	0.06
	6	-	-	-	-	-	-	0.00	0.00	0.01	0.01	0.01	0.01	0.02	0.02	0.03
	7	-	-	-	-	-	-	-	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01
	8	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.01	0.01	0.01
	9	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.01	0.01
	10	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.01
	11	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
	12	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00
	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00
M. paradoxus predators, *M. paradoxus* prey																
Prey age	0	0.00	0.00	0.00	0.01	0.04	0.12	0.26	0.42	0.57	0.70	0.82	0.93	1.03	1.14	1.24
	1	-	0.00	0.00	0.00	0.02	0.05	0.10	0.17	0.23	0.28	0.33	0.37	0.41	0.45	0.49
	2	-	-	0.00	0.00	0.01	0.02	0.04	0.07	0.09	0.11	0.13	0.15	0.16	0.18	0.20
	3	-	-	-	0.00	0.00	0.01	0.02	0.03	0.04	0.04	0.05	0.06	0.07	0.07	0.08
	4	-	-	-	-	0.00	0.00	0.01	0.01	0.01	0.02	0.02	0.02	0.03	0.03	0.03
	5	-	-	-	-	-	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	6	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
	7	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	8	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	9	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00
	10	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00
	11	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
	12	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00
	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00

Table 6.7b: Daily per capita consumption of hake prey (by prey numbers) by hake predators **for the year 2013** (i.e. the last year considered in the model) for the base case.

		Predator age														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
M. capensis predators, *M. capensis* prey																
Prey age	0	0.00	0.02	0.04	0.08	0.13	0.21	0.30	0.42	0.56	0.73	0.91	1.09	1.27	1.43	1.57
	1	-	0.01	0.02	0.03	0.05	0.08	0.12	0.17	0.23	0.30	0.37	0.45	0.52	0.59	0.65
	2	-	-	0.01	0.01	0.02	0.03	0.05	0.07	0.09	0.12	0.15	0.18	0.21	0.23	0.26
	3	-	-	-	0.00	0.01	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10
	4	-	-	-	-	0.00	0.01	0.01	0.01	0.02	0.02	0.02	0.03	0.03	0.04	0.04
	5	-	-	-	-	-	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02
	6	-	-	-	-	-	-	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01
	7	-	-	-	-	-	-	-	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01
	8	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.01	0.01	0.01
	9	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.01
	10	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00
	11	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
	12	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00
	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00
M. capensis predators, *M. paradoxus* prey																
Prey age	0	0.01	0.02	0.06	0.13	0.24	0.40	0.64	0.95	1.37	1.90	2.56	3.31	4.15	5.03	5.93
	1	-	0.01	0.02	0.05	0.09	0.15	0.24	0.36	0.52	0.72	0.97	1.26	1.58	1.92	2.26
	2	-	-	0.01	0.02	0.03	0.05	0.08	0.13	0.18	0.25	0.34	0.44	0.55	0.67	0.79
	3	-	-	-	0.00	0.01	0.02	0.02	0.04	0.05	0.07	0.10	0.13	0.16	0.20	0.23
	4	-	-	-	-	0.00	0.00	0.01	0.01	0.01	0.02	0.03	0.03	0.04	0.05	0.06
	5	-	-	-	-	-	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.02	0.02	0.03
	6	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01
	7	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
	8	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	9	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00
	10	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00
	11	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
	12	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00
	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00
M. paradoxus predators, *M. paradoxus* prey																
Prey age	0	0.00	0.00	0.00	0.01	0.04	0.12	0.27	0.47	0.68	0.90	1.13	1.36	1.61	1.86	2.12
	1	-	0.00	0.00	0.00	0.01	0.04	0.10	0.18	0.26	0.34	0.43	0.52	0.61	0.71	0.81
	2	-	-	0.00	0.00	0.01	0.02	0.04	0.06	0.09	0.12	0.15	0.18	0.21	0.25	0.28
	3	-	-	-	0.00	0.00	0.00	0.01	0.02	0.03	0.04	0.04	0.05	0.06	0.07	0.08
	4	-	-	-	-	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.02	0.02	0.02
	5	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01
	6	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	7	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	8	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	9	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00
	10	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00	0.00
	11	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00	0.00
	12	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	0.00
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00
	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00

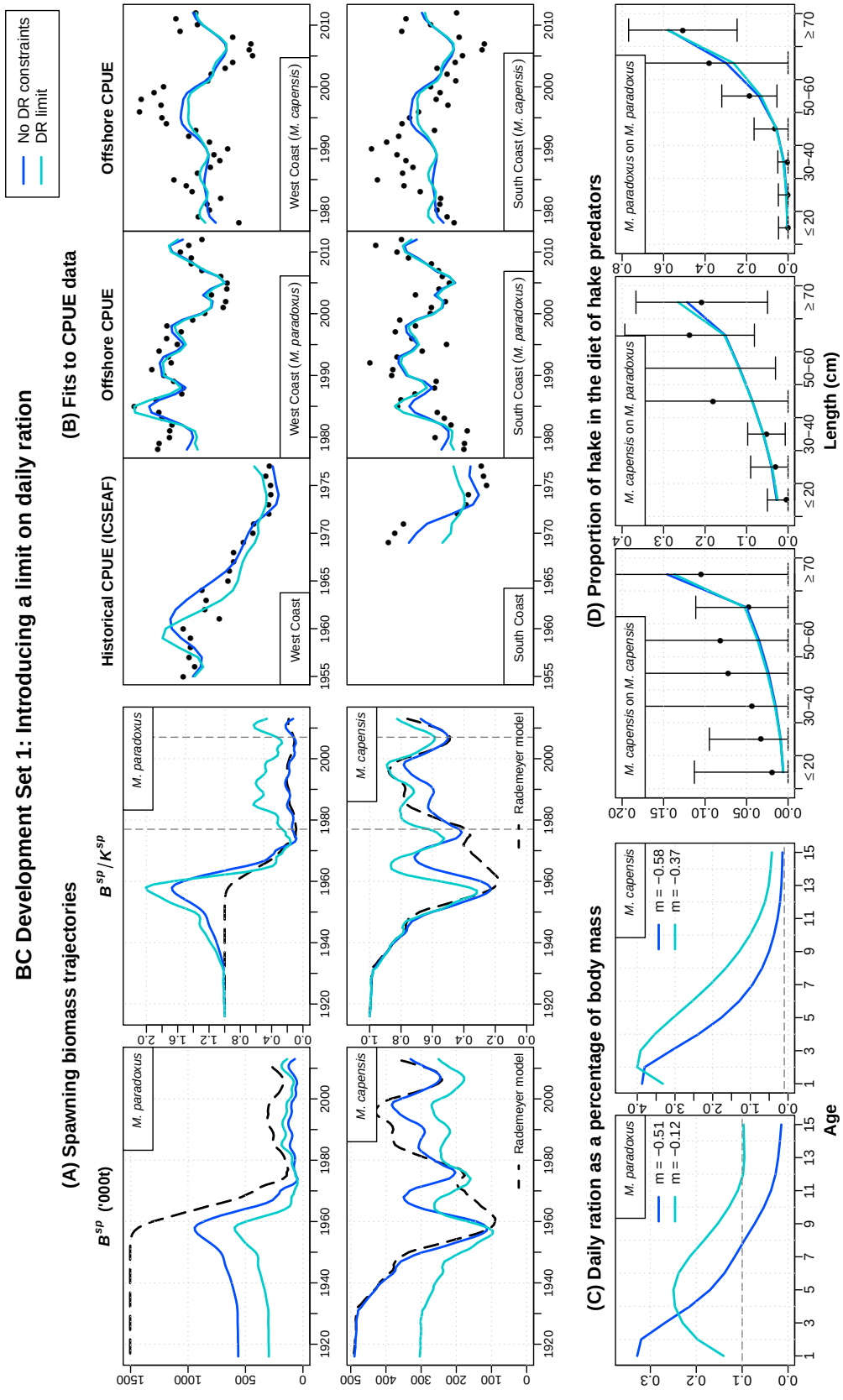


Figure 6.1: Summary plots of the results of the first set of models explored in the base case model development phase. For the first model (dark blue line), no constraints on daily ration (DR) are imposed, whereas for the second (light blue line) a lower (0.1%) and upper (4%) limit are imposed on the daily ration as a percentage of body mass. This Figure, and all the following Figures, show (A) the spawning biomass trajectories in absolute terms in thousand tons and relative to pre-exploitation biomass, (B) the fits to the commercial CPUE data, (C) the daily ration as a percentage of body mass, and (D) the fits to the proportions of hake in the diet of hake predators (with the 95% confidence intervals estimated from the diet data indicated by the error bars). The m values under the legends of the daily ration plots are the slopes of the regressions of the log of daily ration against the log of body mass. In Block A, the vertical dashed lines in the B^{sp}/K^{sp} plots mark 1977 and 2007, two years where the fishery experienced severely low catch rates. Note that "Rademeyer model" has been used to refer to the Rademeyer and Butterworth (2014b) model.

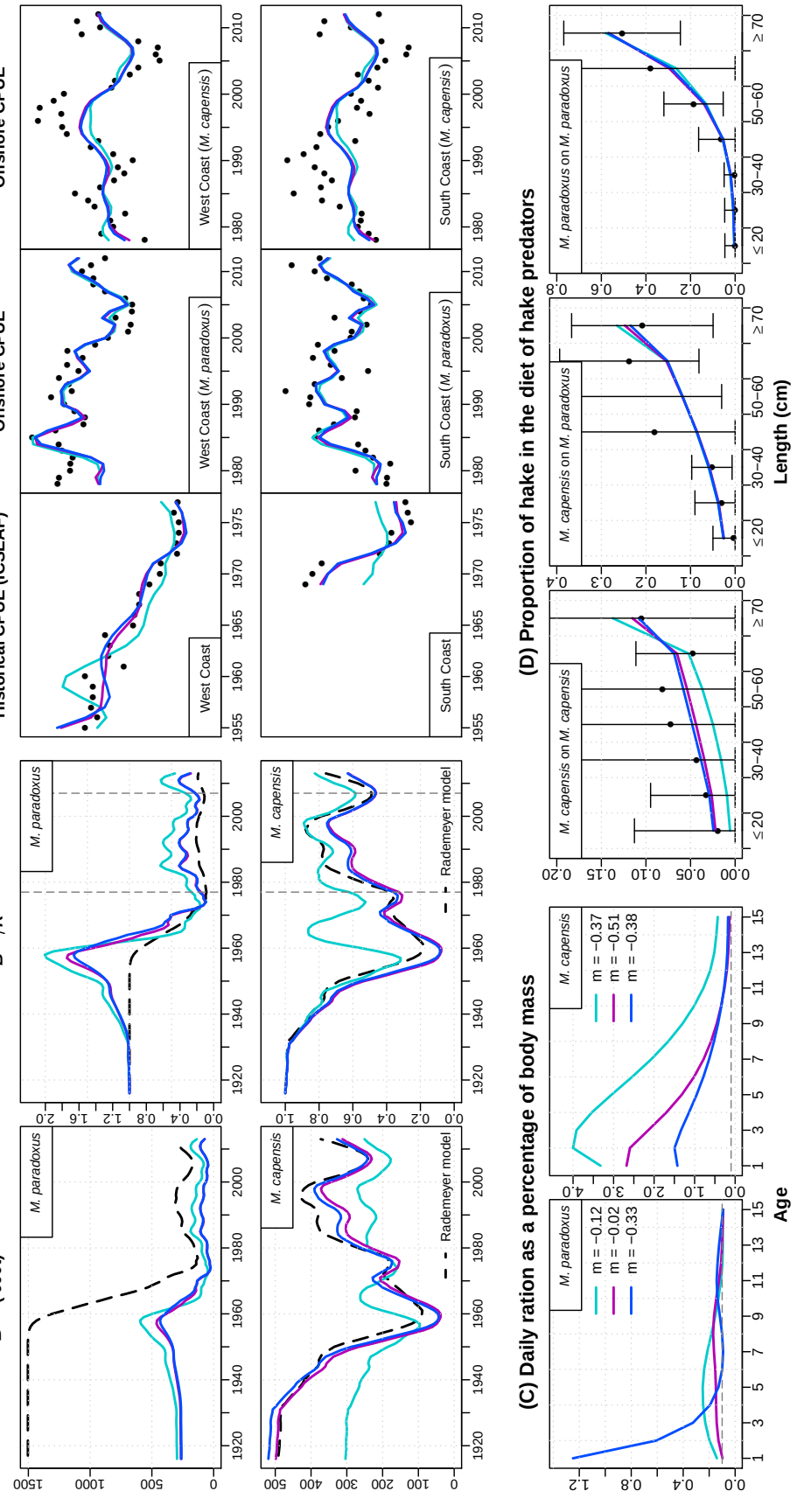


Figure 6.2: Summary plot of the results of the second set of models explored in the base case development phase. The first model (light blue line) imposes a limit on daily ration and is the same as the model shown by the light blue line in the previous Figure. The second model (purple line) introduces a depth-availability vector to allow the *M. capensis* predators to consume more *M. paradoxus* prey as the predators grow and move into deeper waters (see Section 5.5.2). The third model (dark blue line) adds a penalty to the negative log-likelihood to force the gradient of the regression of the log of the daily ration against the log of the predator weight to lie close to -1/3 (see Equation 5.36). The values of these regression slopes are indicated under the legends of the daily ration plots in Block C.

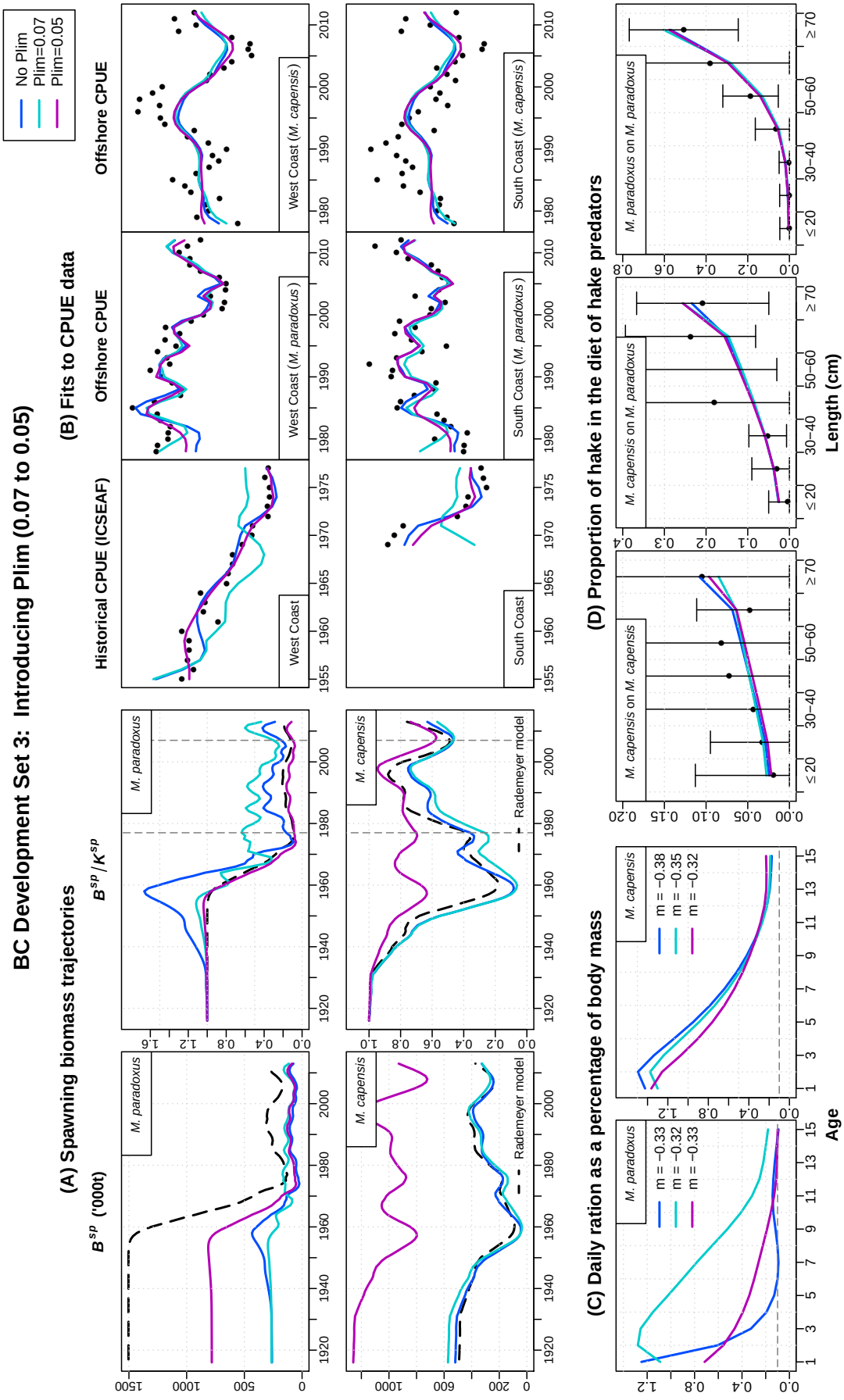


Figure 6.3: Summary plots of the third set of models explored in the base case development phase. These models, as well as those in the next Figure, introduce a predator competition aspect by limiting the predation mortality rate P. The models in this Figure show the results for no P_{lim} (which is the same as the "Slope DR" model in the previous Figure), for $P_{lim} = 0.07$ and for $P_{lim} = 0.05$.

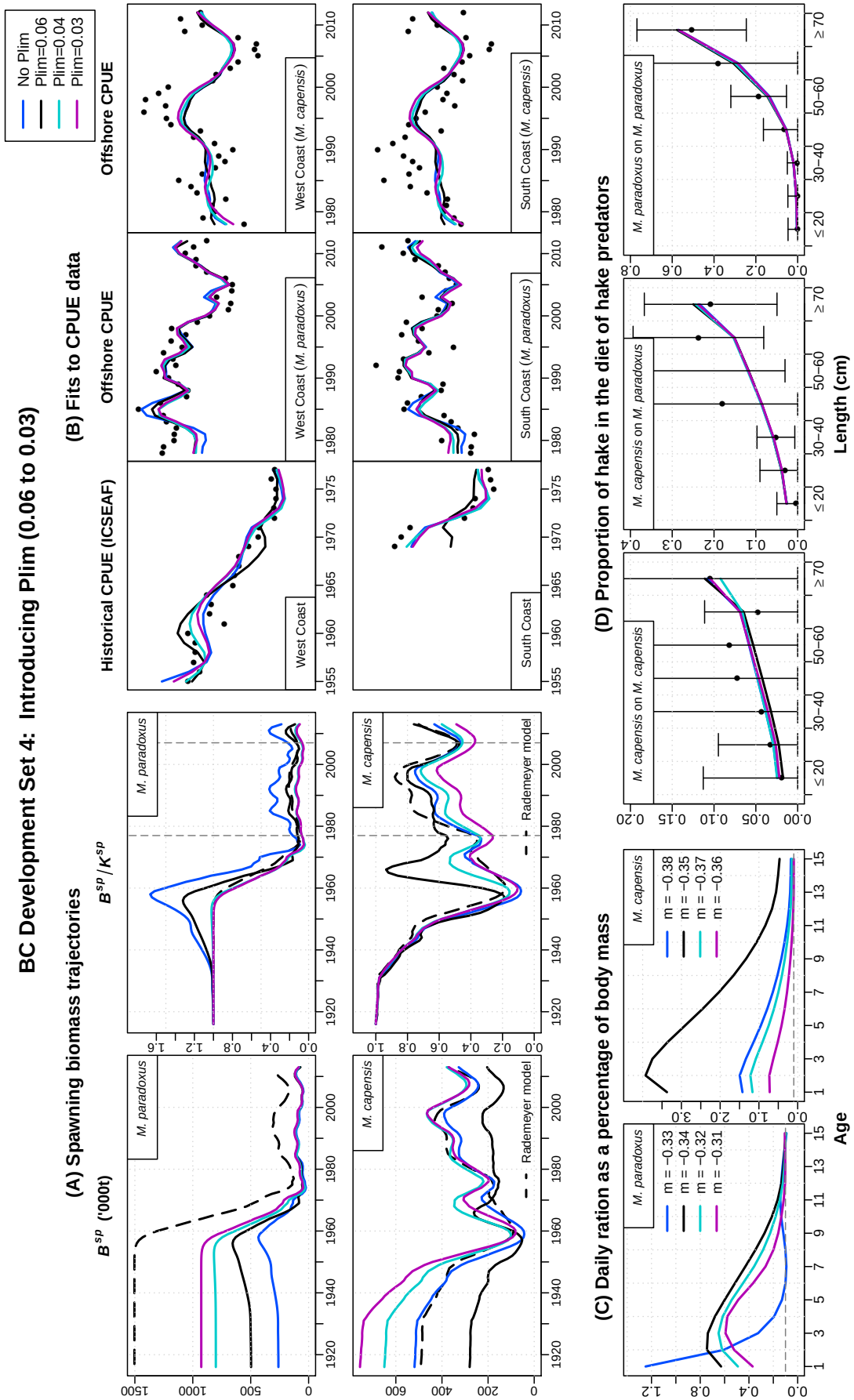


Figure 6.4: The models presented in this Figure continue the exploration of different P_{lim} values, namely $P_{lim} = 0.06$, $P_{lim} = 0.04$ and $P_{lim} = 0.03$. The no P_{lim} model is repeated from the previous Figure. Note that the $P_{lim} = 0.06$ (black solid line) is the final choice for the base case.

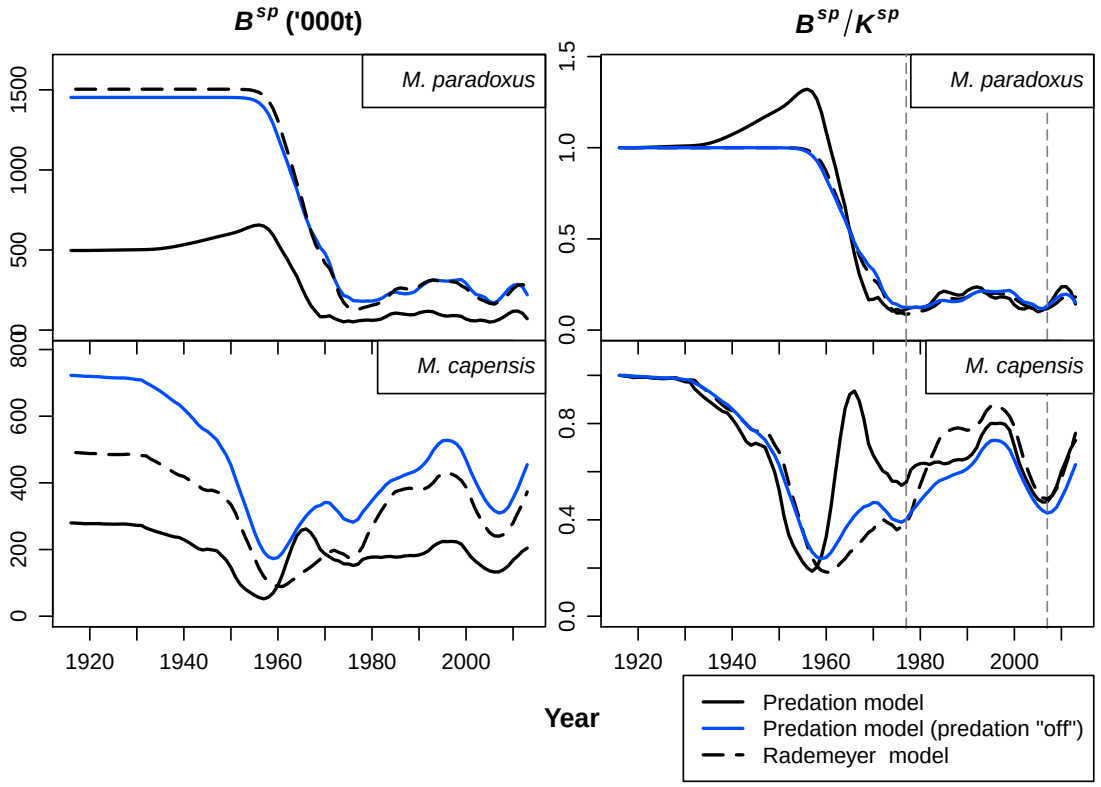


Figure 6.5a: Spawning biomass trajectories are shown for the base case predation model (solid black line), for the predation model with predation "off" (solid blue line), and for the Rademeyer and Butterworth (2014b) model (dashed black line). The left panel shows the spawning biomass in absolute terms in thousand tons, while the right panel shows the trajectories relative to the pre-exploitation spawning biomass. The two vertical dashed lines in the right panel mark the years 1977 and 2007, years where the fishery was experiencing severe problems with low catch rates.

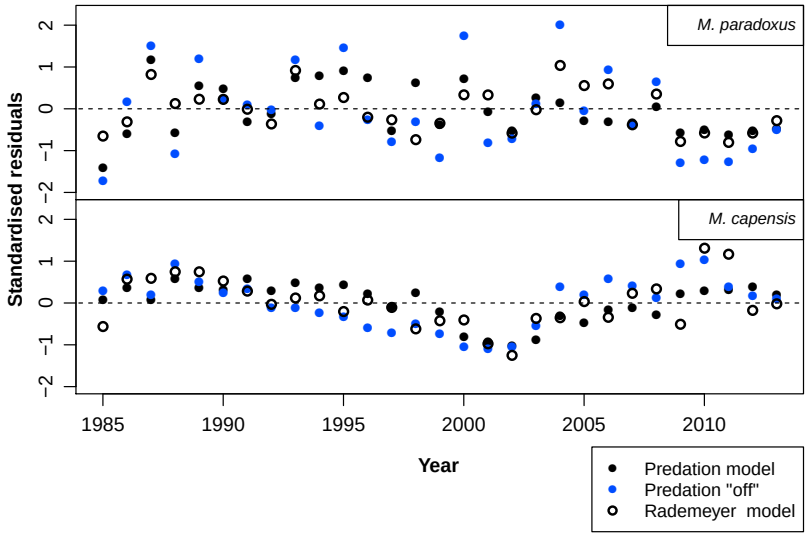


Figure 6.5b: Stock-recruitment residuals estimated for the years 1985-2013 by the base case predation model, the predation "off" model and the Rademeyer and Butterworth (2014b) model. The residuals have been standardised by dividing by σ_R (see Section 4.3.5 for the details of σ_R).

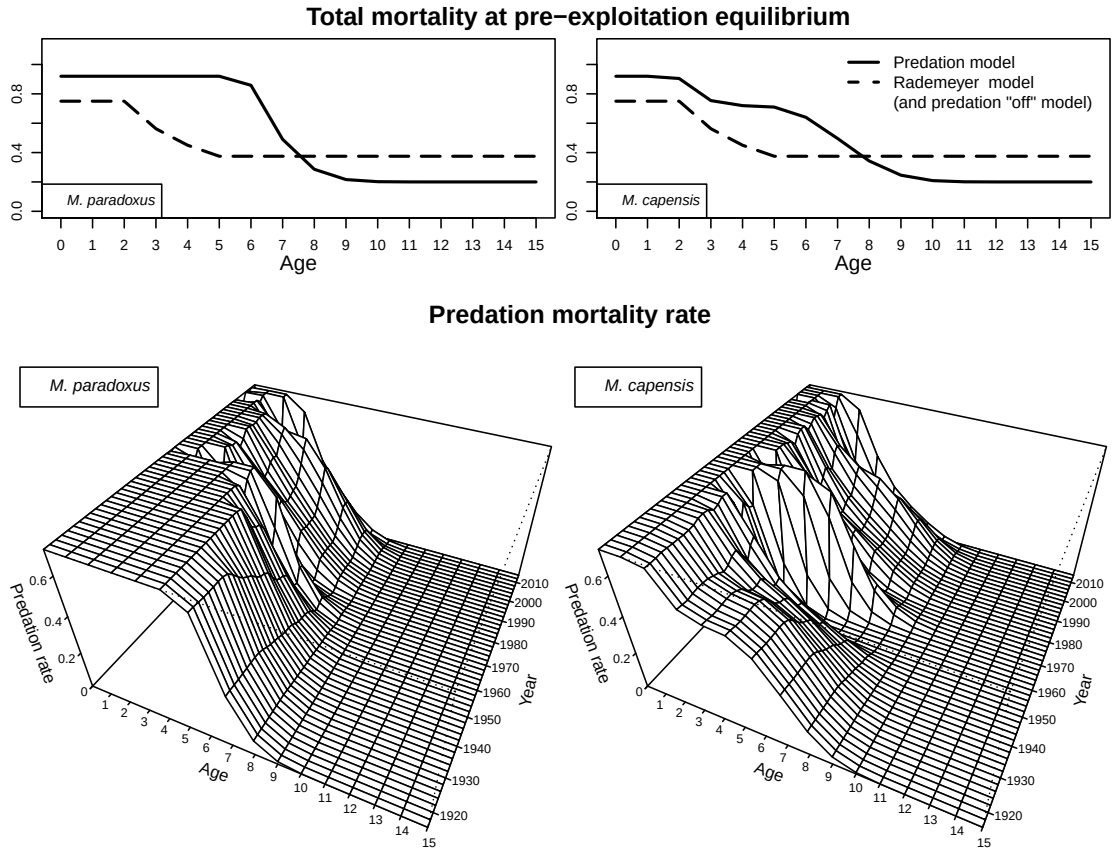


Figure 6.5c: The top panel shows the total mortality as a function of age (in yr^{-1}) at pre-exploitation equilibrium for the base case predation model (solid black line) and for the Rademeyer and Butterworth (2014b) model. The natural mortality rates for the predation model with predation "off" is set equal to the Rademeyer and Butterworth (2014b) natural mortality values. The two plots on the bottom show a three-dimensional graphical representation of the predation mortality rates by age and year.

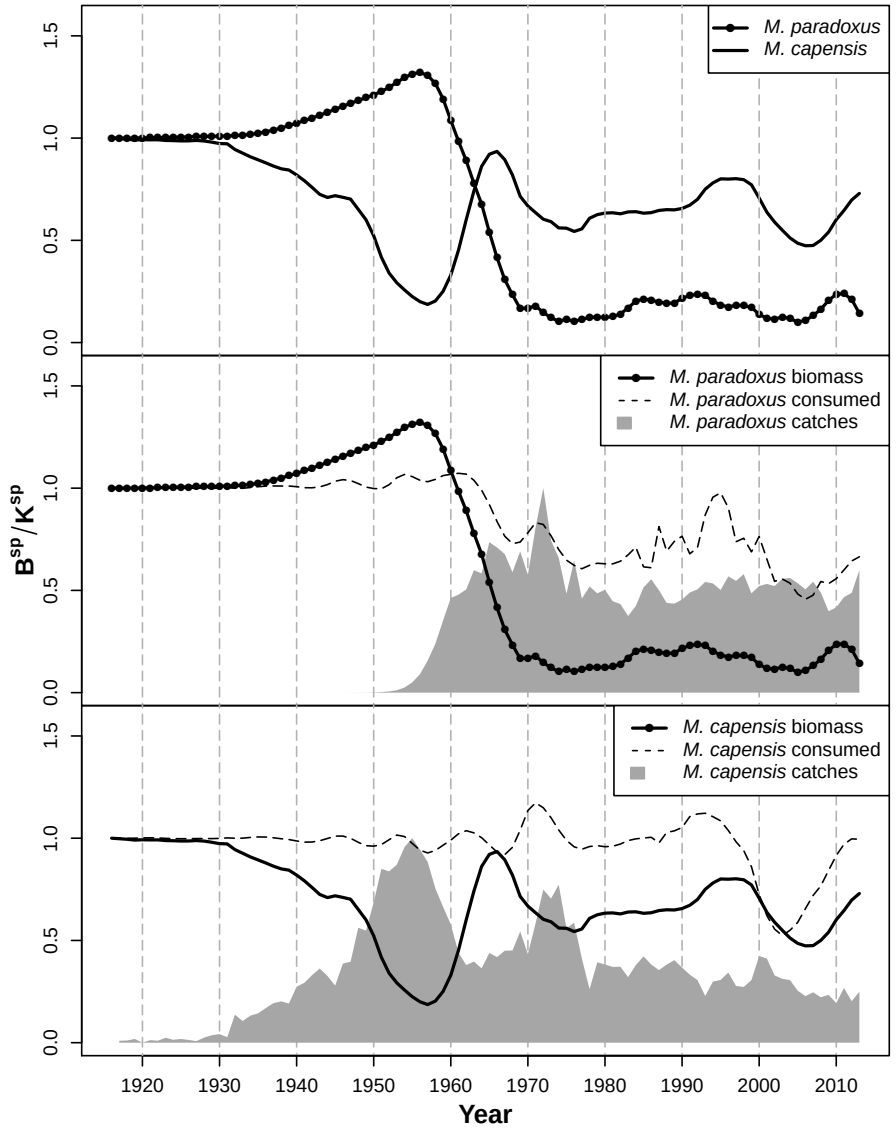


Figure 6.5d: Depletion levels are shown in the form of spawning biomass trajectories relative to pre-exploitation equilibrium (B^{sp}/K^{sp}) for the base case predation model. The top plot superimposes the trajectories for the two species. The middle plot superimposes the *M. paradoxus* spawning biomass trajectory, as well as the total number of *M. paradoxus* hake consumed yearly by hake predators (relative to the number consumed at equilibrium), onto the total commercial catches for this species. The bottom plot does the same for the *M. capensis* trajectory, number of hake consumed and catches. Note that the catches have been scaled so that the maximum is one for each species.

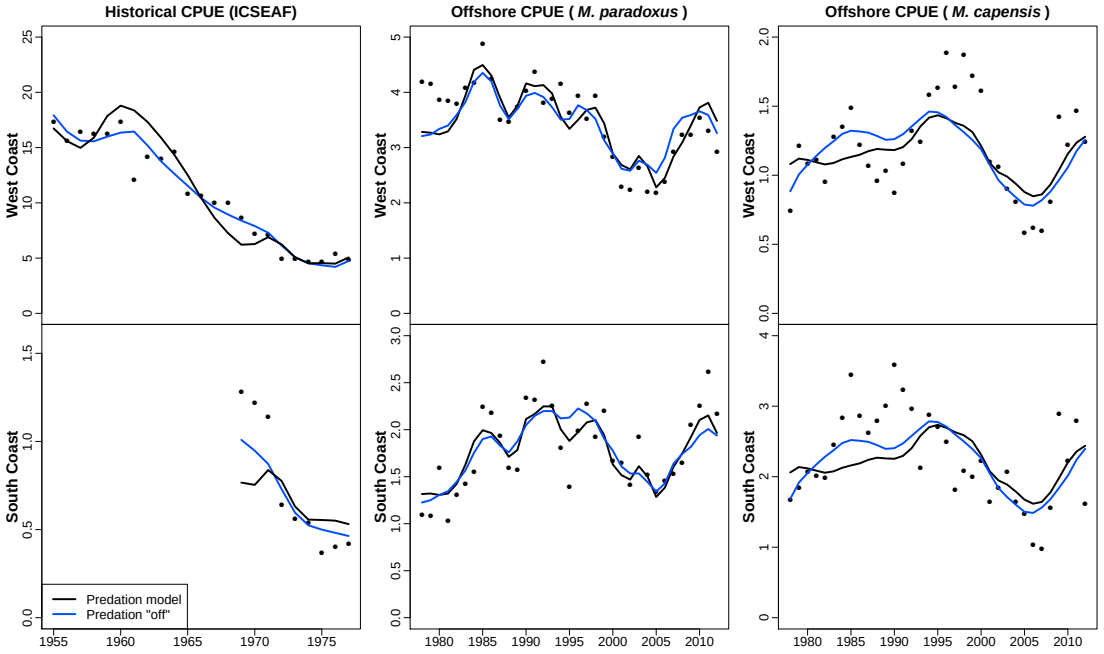


Figure 6.5e: Fits to the commercial CPUE are shown for the base case predation model (black lines) and for the predation model with predation "off" (blue lines). Fits are shown for the historical ICSEAF CPUE and for the more recent GLM-standardised offshore CPUE. The units of these series are specified in Table 3.2.

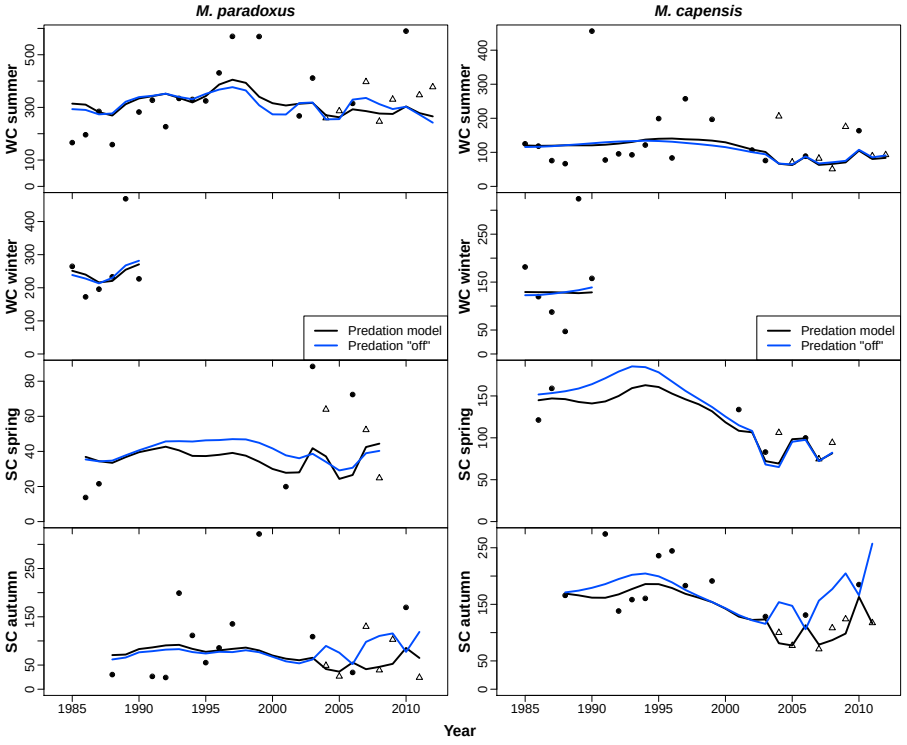


Figure 6.5f: Fits to the survey abundance indices are shown for the base case predation model (black lines) and for the predation model with predation "off" (blue lines). Triangles have been used to indicate years for which the new gear was used in the surveys, and circles for all other years. In the axis labels, "West Coast" has been abbreviated as "WC", and "South Coast" as "SC". The units are in thousand tons.

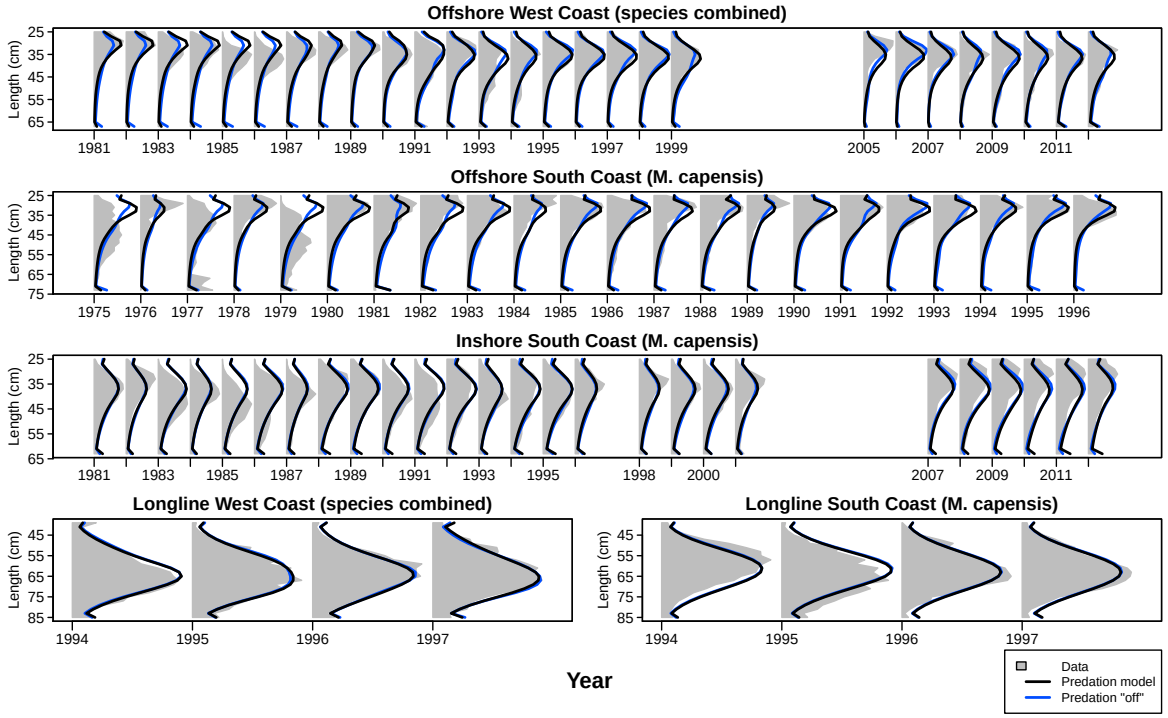


Figure 6.5g: Fits to species-combined (or *M. capensis* only) commercial catch-at-length data are shown by year and fleet. The observed distributions from the commercial catches are indicated by the grey shaded areas, and the solid black and blue lines respectively show the fit of the base case predation model and the predation "off" model.

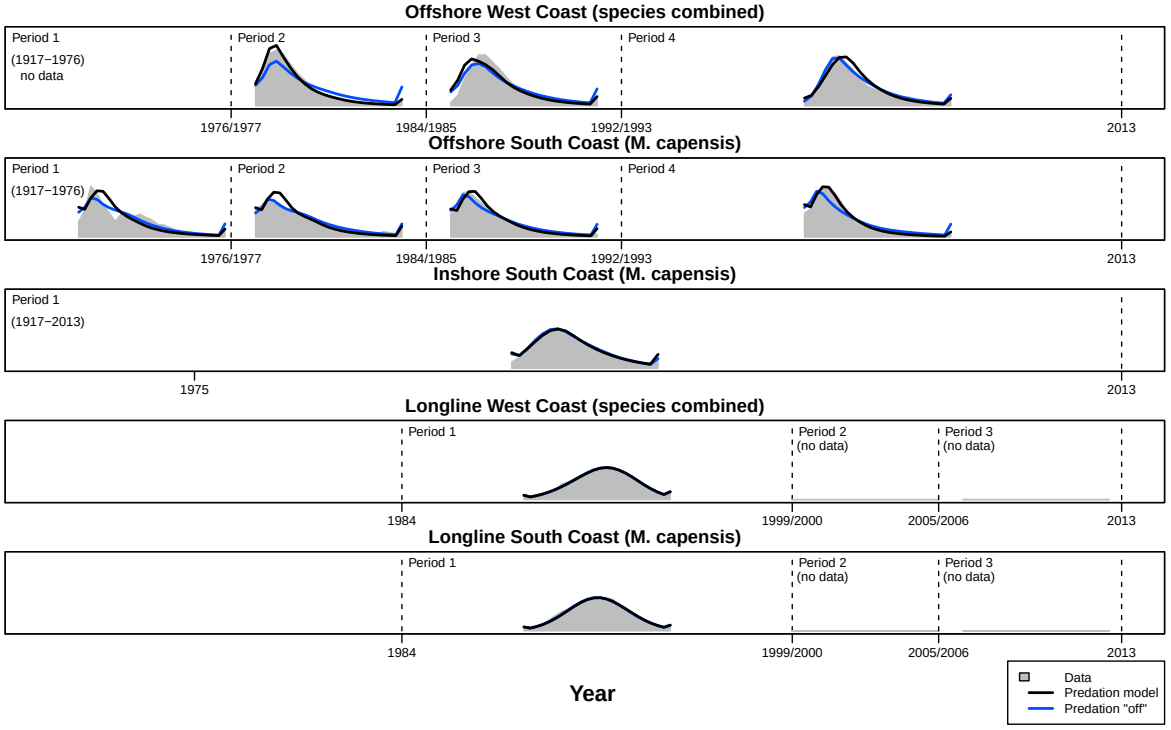


Figure 6.5h: Repeat of the catch-at-length fits in Figure 6.5g, but with observed data and model estimates aggregated over the periods for which separate selectivities are estimated.

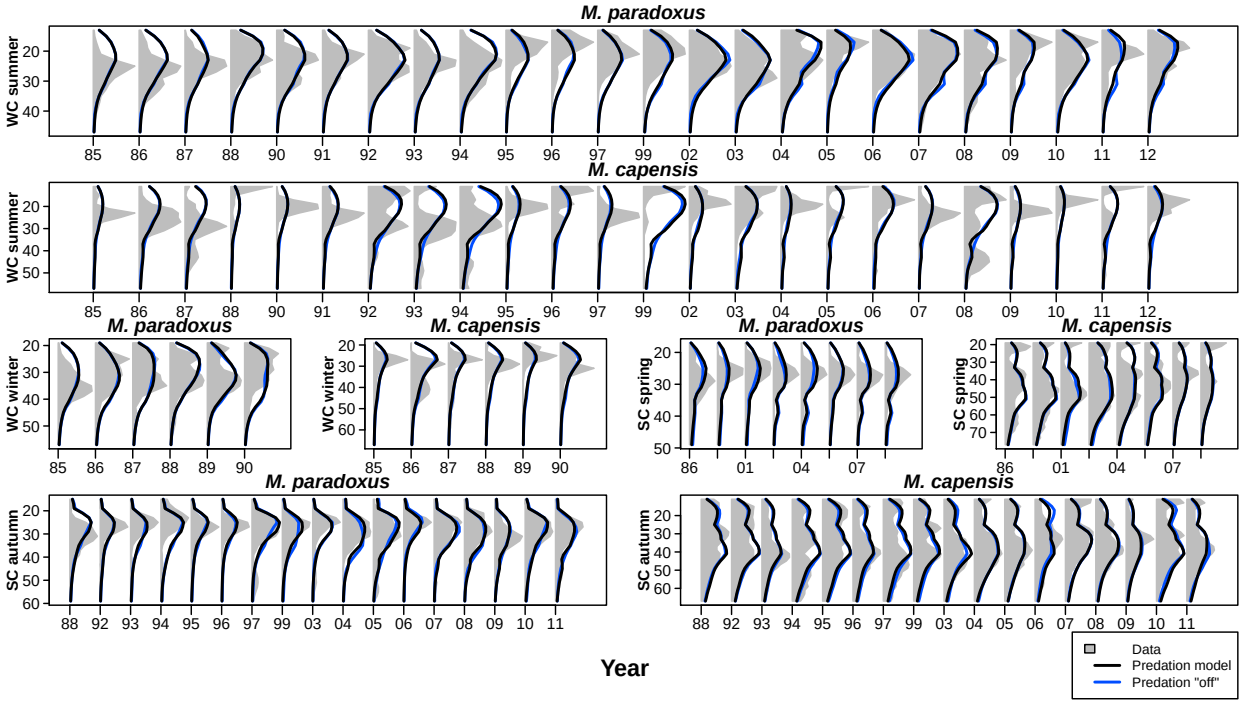


Figure 6.5i: Fits to the survey catch-at-length data are shown for each survey and species. The grey shaded areas indicate the observed data, while the black and blue lines respectively show the fits of the base case predation model and the predation "off" model.

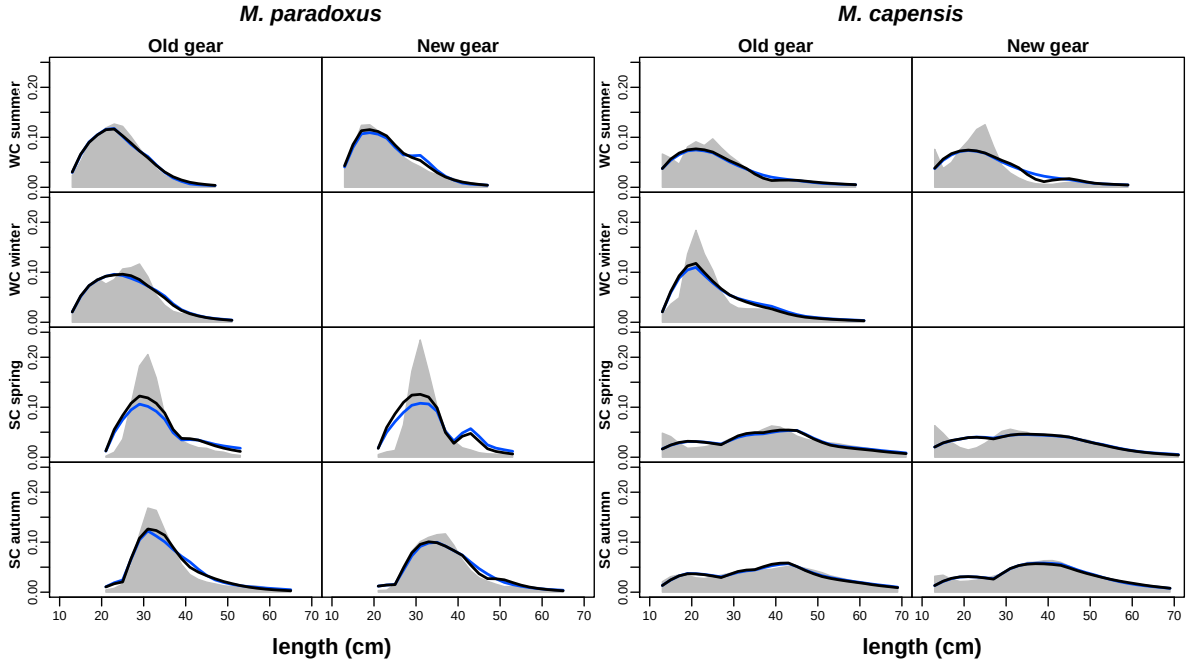


Figure 6.5j: Repeat of the catch-at-length fits shown in Figure 6.5i, but with the observed data and model estimates aggregated over the years for which the old gear and new gear, respectively, were used with separate selectivities are estimated. Note that the seemingly worse fits to the year-disaggregated catch-at-length data in Figure 6.5i (especially in comparison to the fits to the disaggregated commercial data in Figure 6.5g) are a result of the relatively high inter-annual variance and low sample sizes of the survey data.

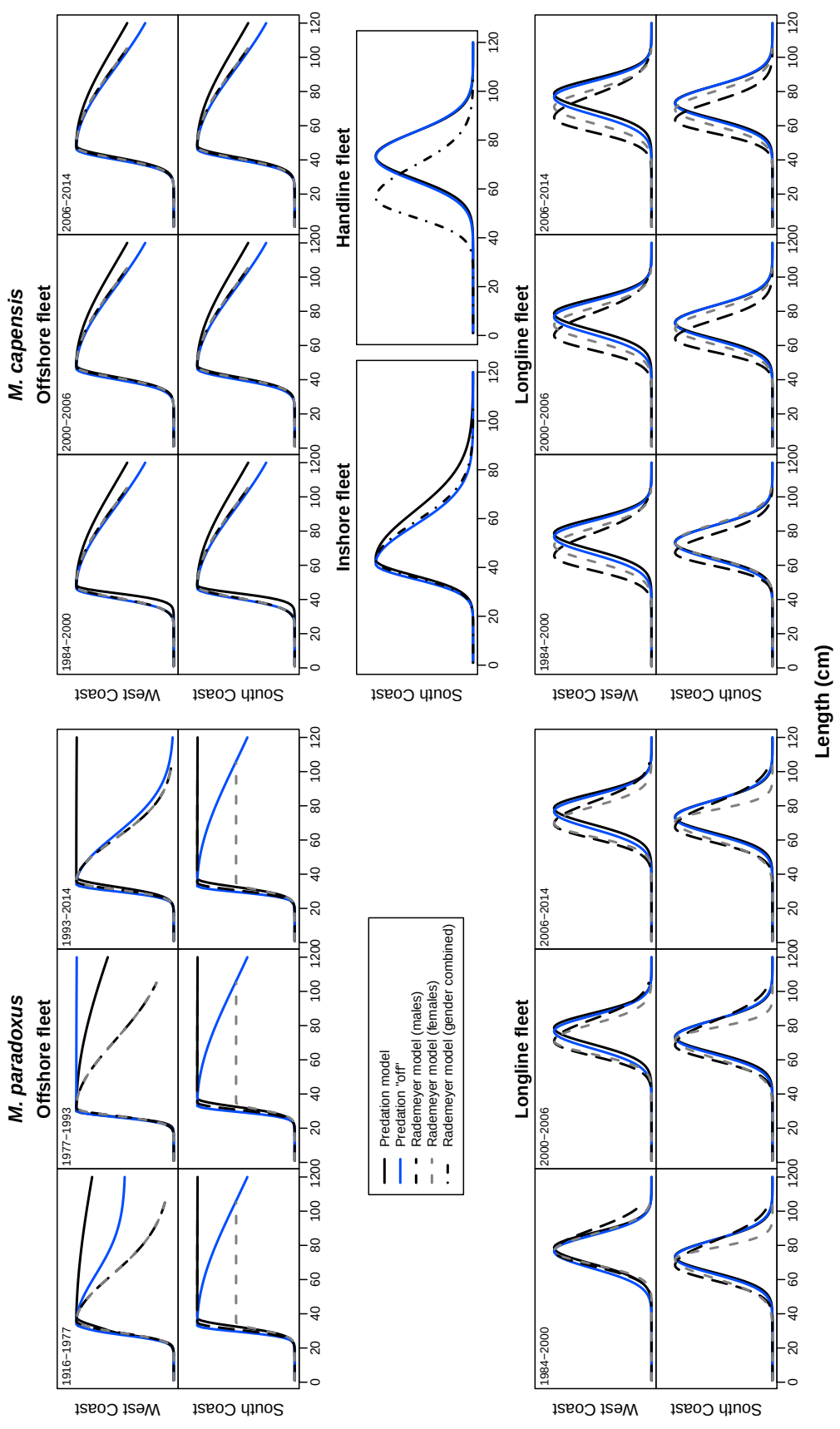


Figure 6.5k: Estimated selectivities-at-length for the various fishing fleets are shown for the predation model (solid black line), the predation "off" model (solid blue line) and the Rademeyer and Butterworth (2014b) model (dashed black lines for males, dashed grey lines for females, and dash-dotted black line for gender combined selectivities). The South Coast inshore and handline fleets are assumed to catch *M. capensis* only. The Rademeyer and Butterworth (2014b) model estimates a separate longline selectivity for each of three periods, each coast and each species, but the predation model estimates only one selectivity per coast and takes theses selectivities to be the same for both species. Furthermore the Rademeyer and Butterworth (2014b) model takes the handline to be the average between South Coast longline and South Coast inshore *M. capensis* parameters, while the predation and predation "off" models have assumed the same parameters as for the South Coast longline selectivity.

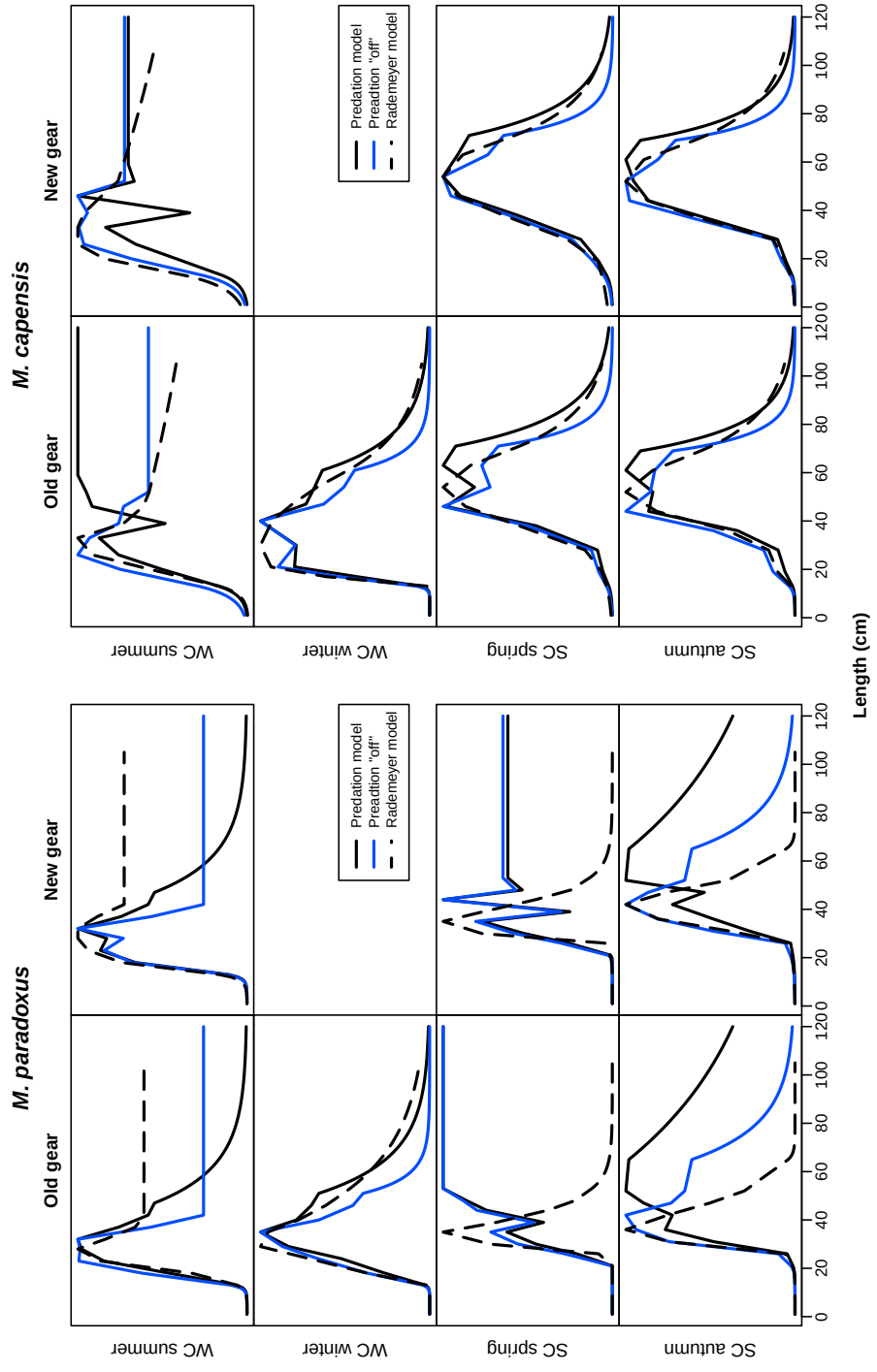


Figure 6.5l: Survey selectivities-at-length estimated by the predation model (solid black line), the predation "off" model (solid blue line) and the Rademeyer and Butterworth (2014b) model (dashed black lines). The selectivities estimated for surveys using the new gear are shown separately to those estimated for the surveys using the old gear. "WC" stands for "West Coast" and "SC" for South Coast.

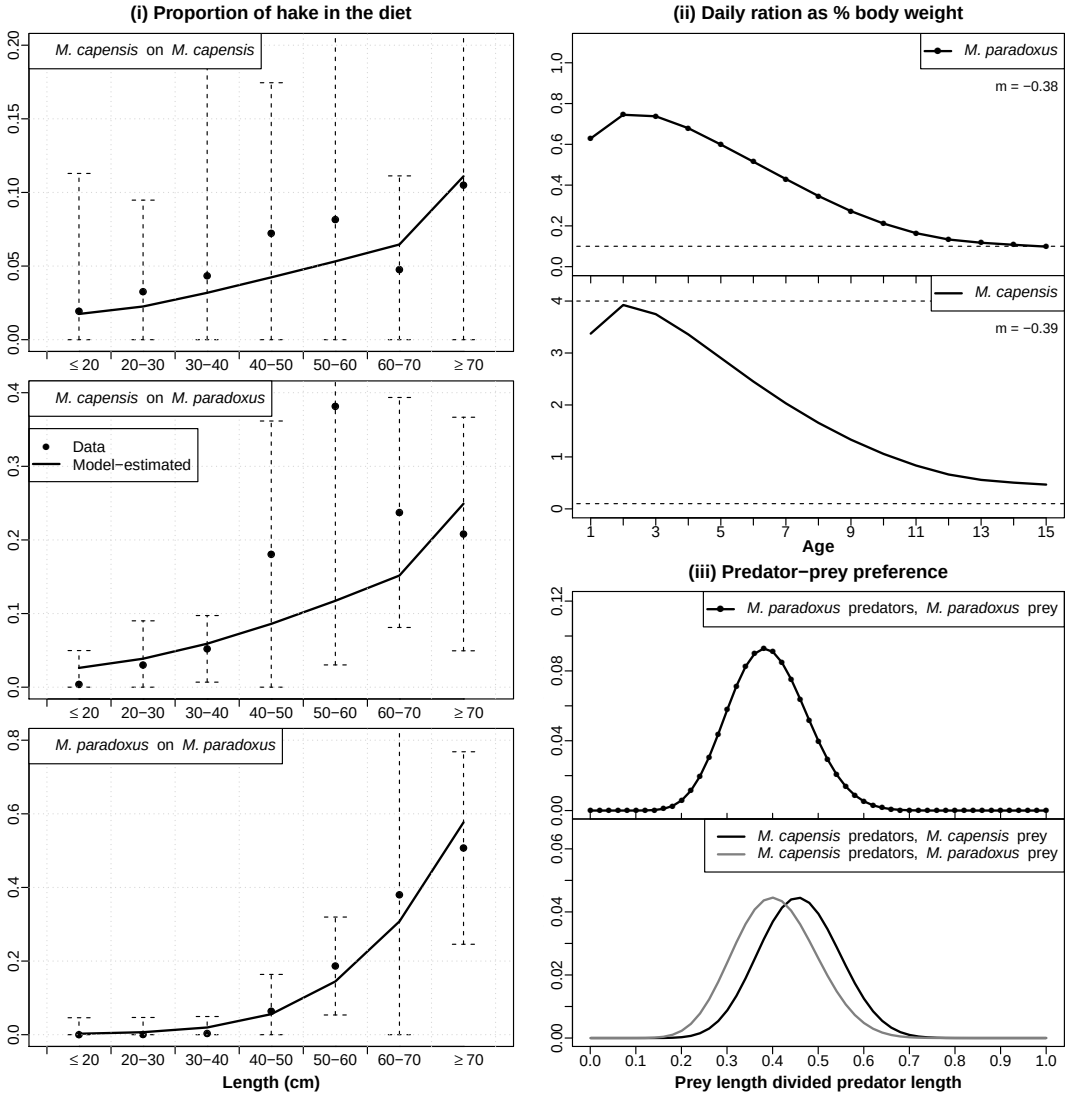


Figure 6.5m: Three diet-related quantities are shown for the base case predation model. The three Figures on the left show the proportion of hake in the diet of hake predators for each predator-prey pairing. The proportions derived from the diet data are indicated by the closed circles, and their 95% confidence intervals (twice the standard deviation) are shown by the dashed error bars. The solid black lines show the model fits. Note that the vertical axes are not to the same scale. The top two Figures on the right show the model-estimated daily ration for *M. paradoxus* and *M. capensis*. The upper and lower limit bounds enforced in the model on the daily ration are shown by the dashed lines. The value of the slope of the regression of the log of daily ration against the log of body mass is indicated under the legend. The bottom two Figures on the right show the preference functions estimated by the predation model for each predator-prey pairing. Preference is plotted against the ratio of prey to predator length. For *M. capensis* predators, separate preference functions are shown for *M. capensis* prey (grey line) and *M. paradoxus* prey (black line). *M. paradoxus* is assumed not to consume any *M. capensis* hake prey.

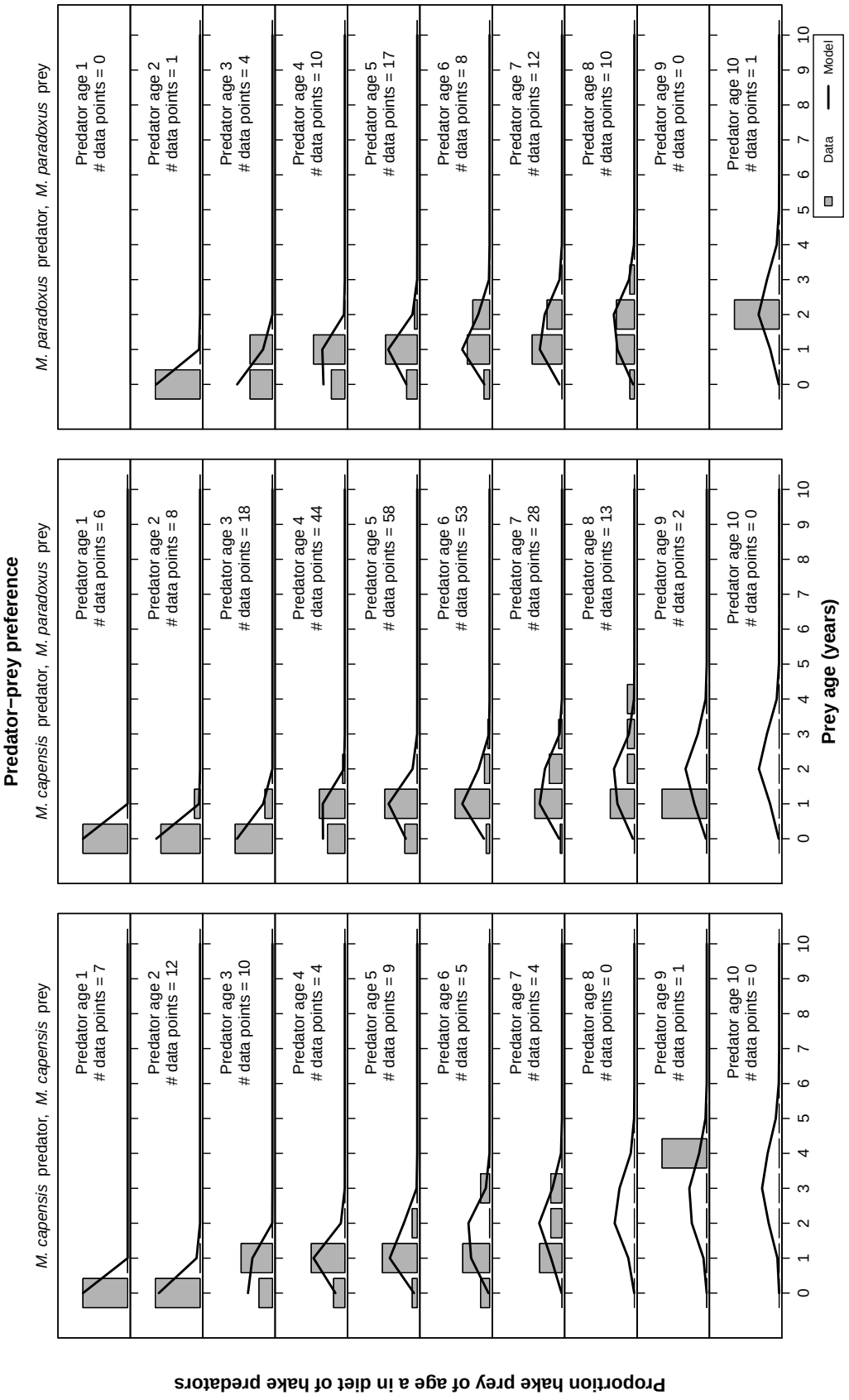


Figure 6.5n: Fits to the preference data are shown for the base case predation model. Each of the three panels corresponds to a different predator-prey pairing, and within each panel predator age increases from top to bottom. The grey bars show the counts of prey items of different ages found in the stomachs of predators of a given age. The ages are calculated from the lengths recorded in the database for the prey items, with the use of the pertinent von Bertalanffy growth curve equation. The numbers of data points corresponding to each predator age are given in the legends. The model fits to the preference data are shown by the solid black lines.

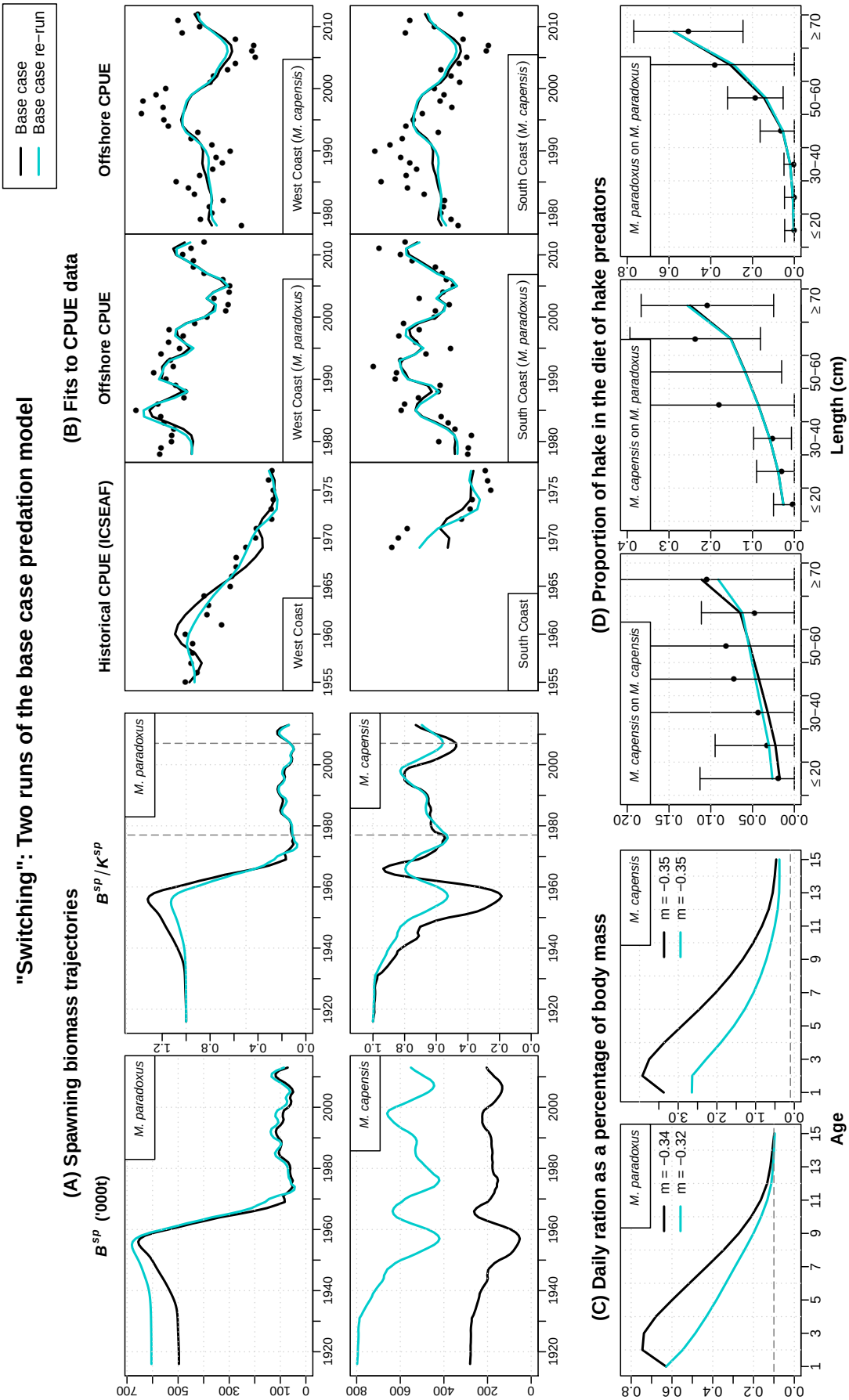


Figure 6.6: Results are shown for the base case and a re-run of the base case with different starting values for the estimable parameters, illustrating how the model can exhibit "switching". This is an example of a "Switch" Type A (see Section 6.4). Note that since this Figure focuses on the "switch" between two variants of the base case predation model, the Rademeyer and Butterworth (2014b) spawning biomass trajectories have not been included here.

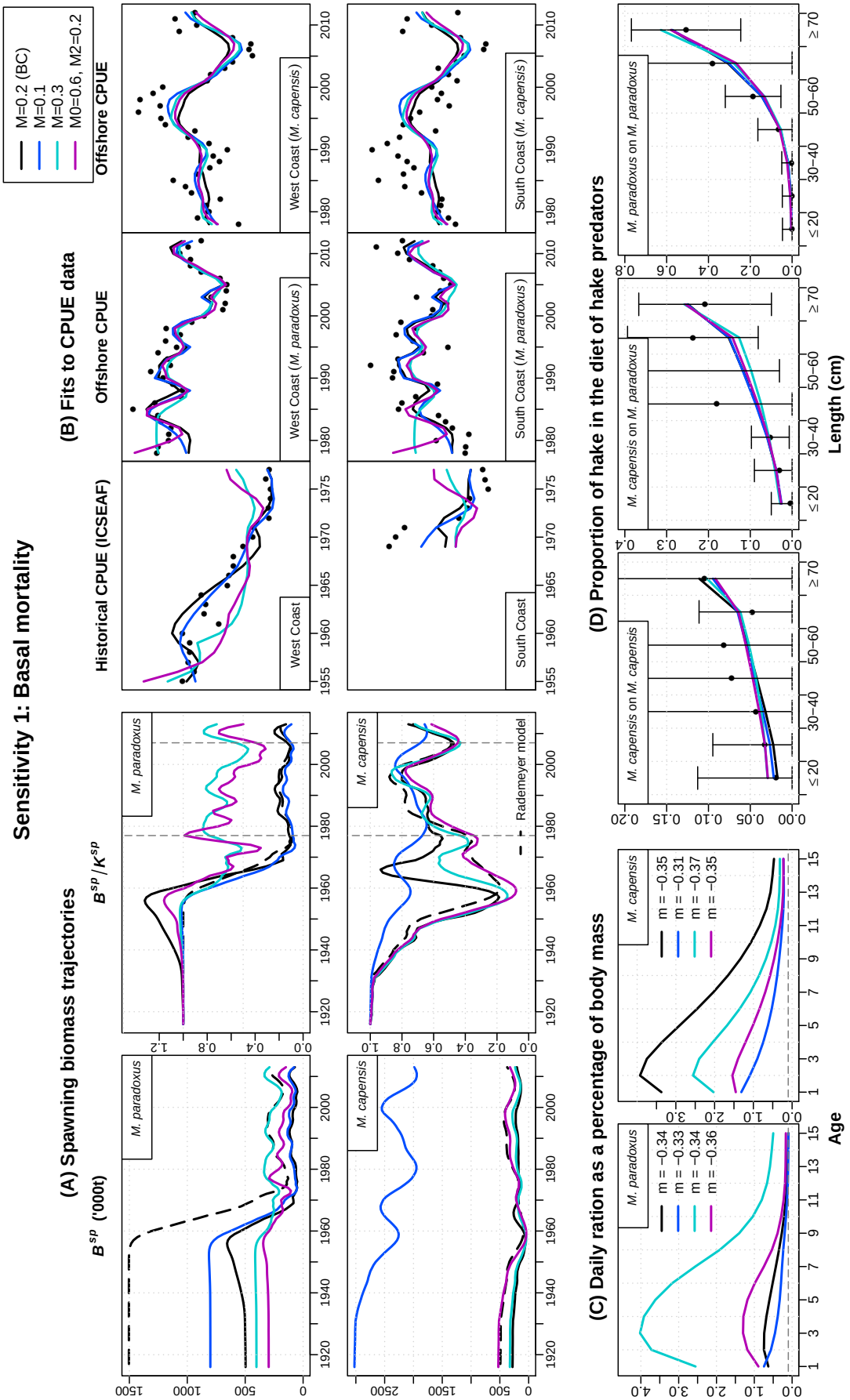


Figure 6.7: Summary plots of the results for the first sensitivity set, which implements different values for the basal mortality, M^b. The black line repeats the base case results ($M^b = 0.2\ yr^{-1}$), while the next two models (dark and light blue lines) implement age-independent basal mortality rates of 0.1 and 0.3 yr^{-1} respectively. The last model (purple line) implements an age-dependent basal mortality, with $M^b = 0.6\ yr^{-1}$ for hake of age zero, dropping linearly to $M^b = 0.2\ yr^{-1}$ for hake aged two.

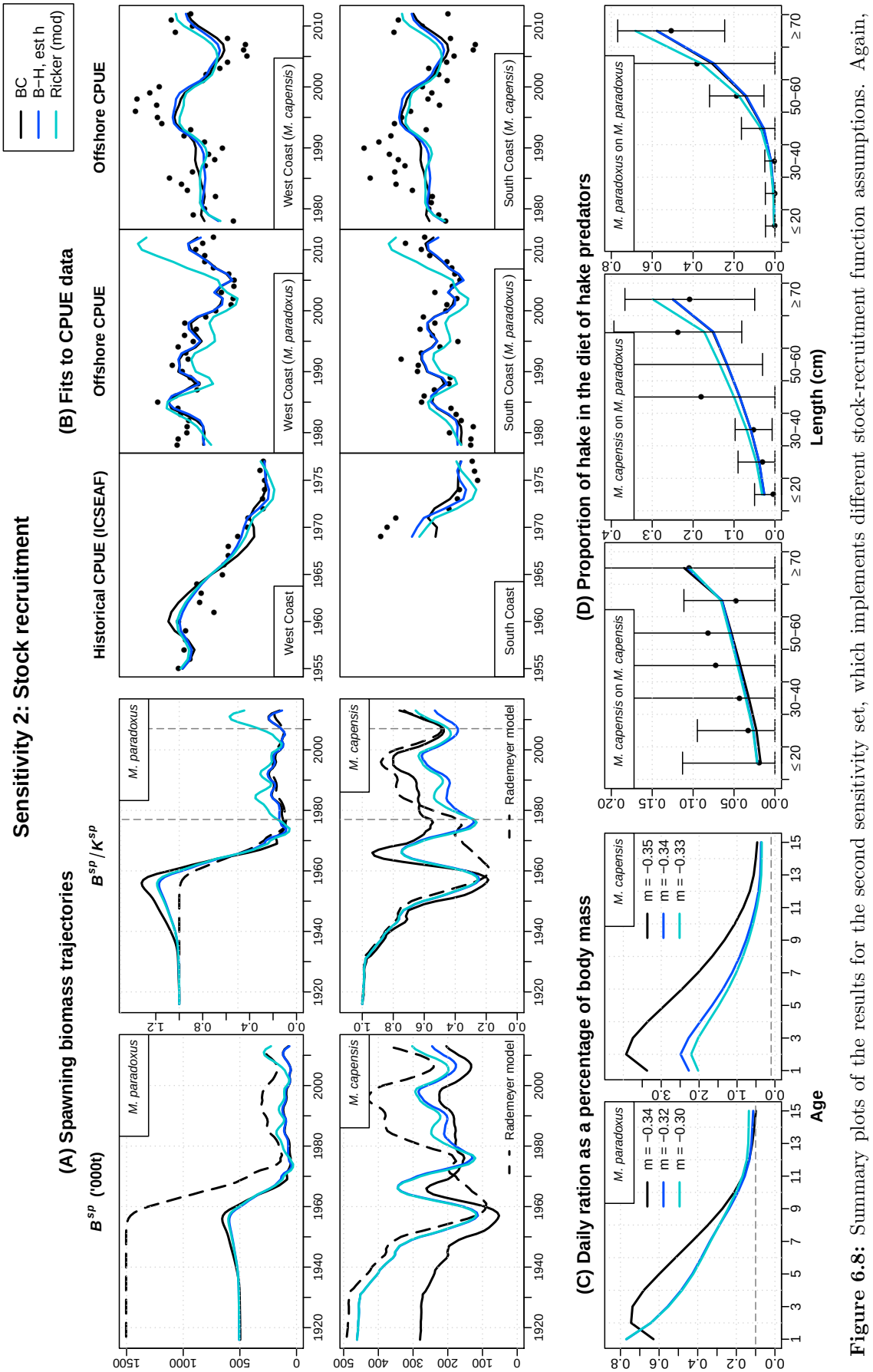


Figure 6.8: Summary plots of the results for the second sensitivity set, which implements different stock-recruitment function assumptions. Again, the base case (BC) is repeated as previously (black line). The first model (dark blue) implements a Beverton-Holt stock-recruitment relationship as for the BC, but estimates the steepness parameter h. The second model (light blue) implements the modified Ricker stock-recruitment relationship (see Equation 6.1).

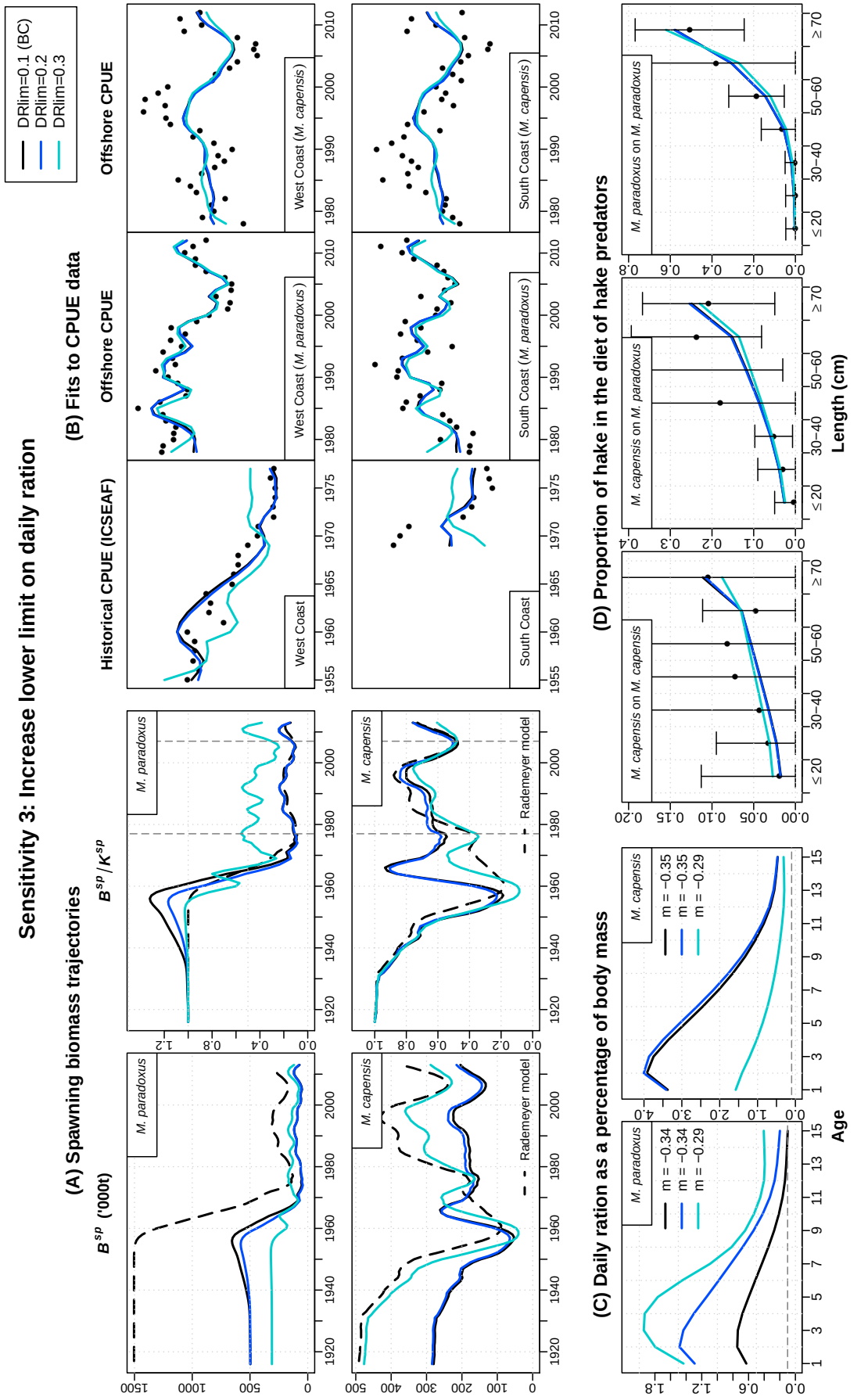


Figure 6.9: Summary plots of the results for the third sensitivity, which increases the lower limit imposed on the daily ration as a percentage of body mass. The base case (black line) imposes a lower limit of 0.1% of body mass, while the other two models shown here impose lower limits of 0.2% and 0.3%.

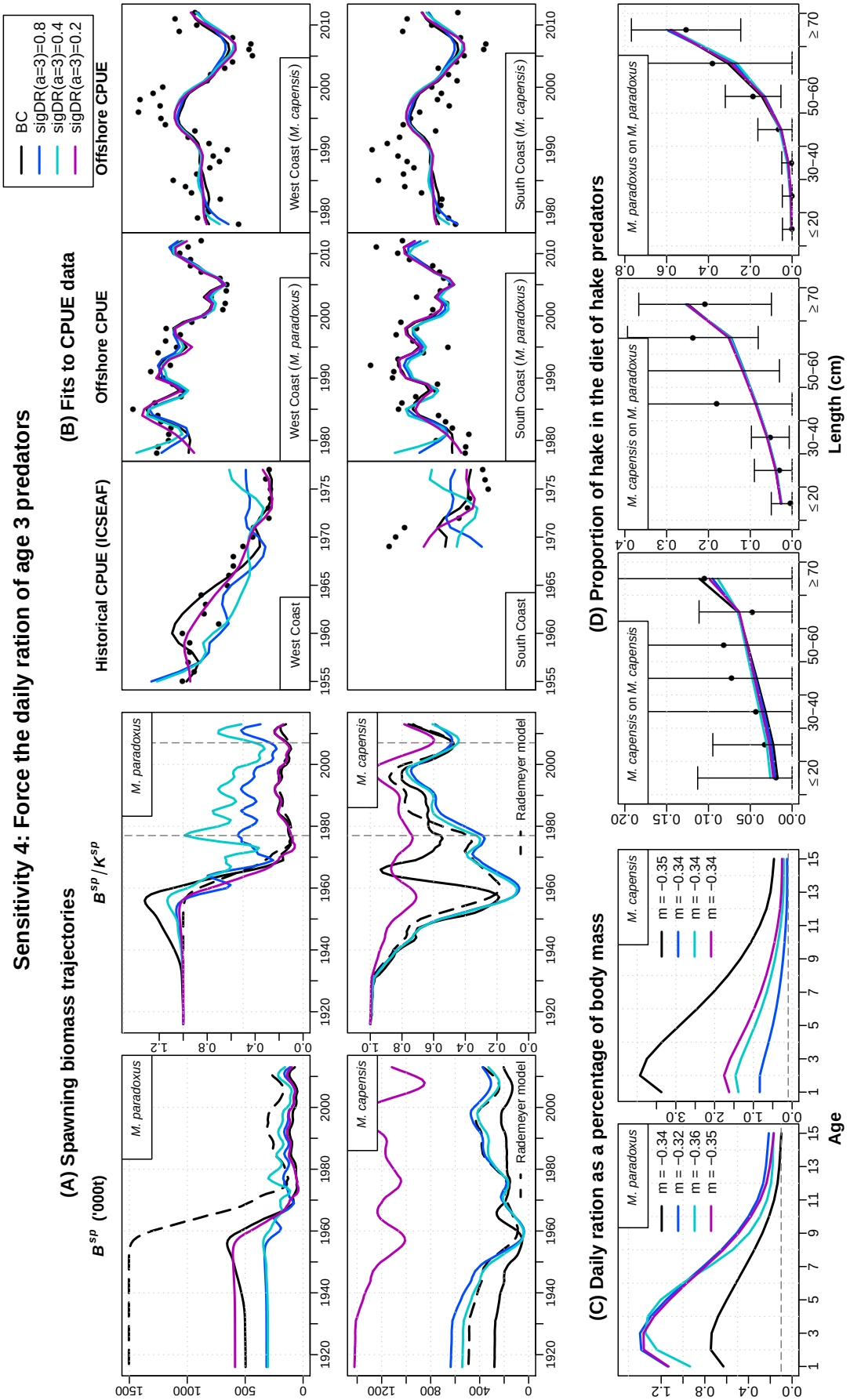


Figure 6.10: Summary plots of the results for the fourth sensitivity set, which introduces a penalty to the negative log-likelihood to force the daily ration of age 3 predators of both species to lie as close to 1.53% of body mass (see Equation 6.2). The various models shown in the Figure reflect different variances for the value of 1.53% (and thus different weights for this penalty in the negative log-likelihood).

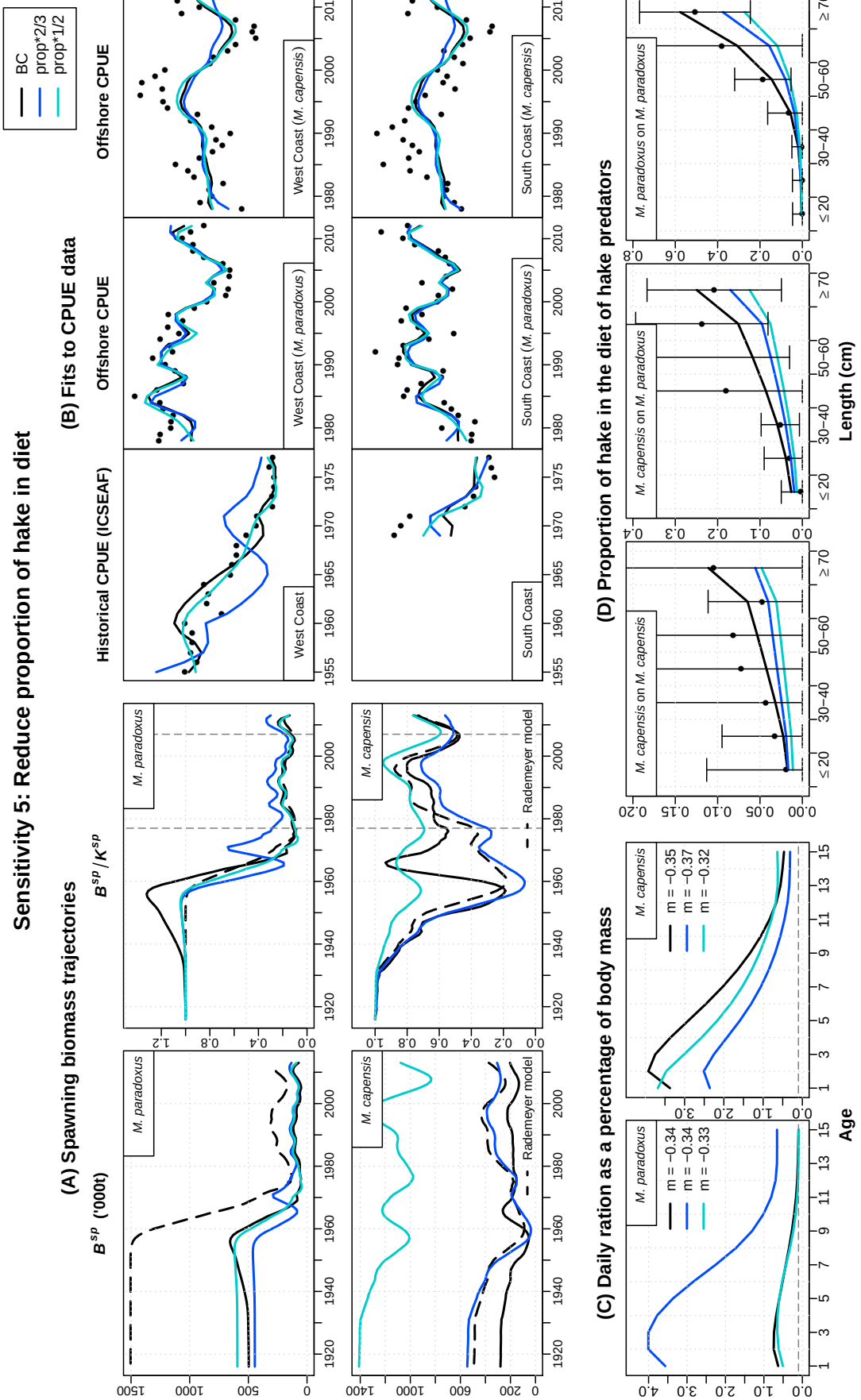


Figure 6.11: Summary plots of the results for fifth sensitivity set. The two models shown here alongside the base case reduce the proportion of hake in the diet to which the model tries to fit. The first model (dark blue) multiplies the proportions and their associated standard errors by 2/3 and the second model (light blue) multiplies these by 1/2.

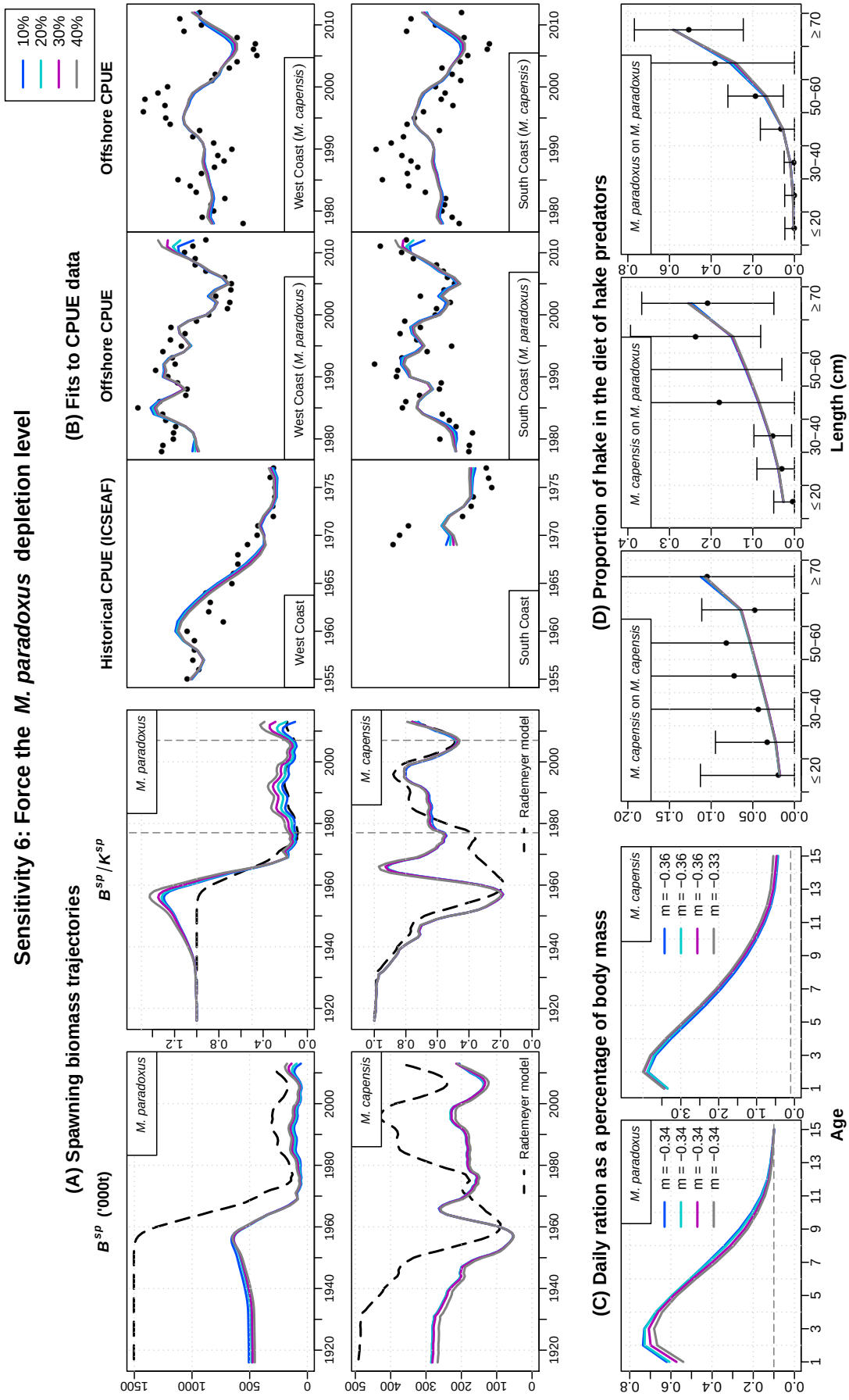


Figure 6.12: Summary plots of results for the sixth sensitivity set, which forces different levels of depletion in 2013 for the *M. paradoxus* population.

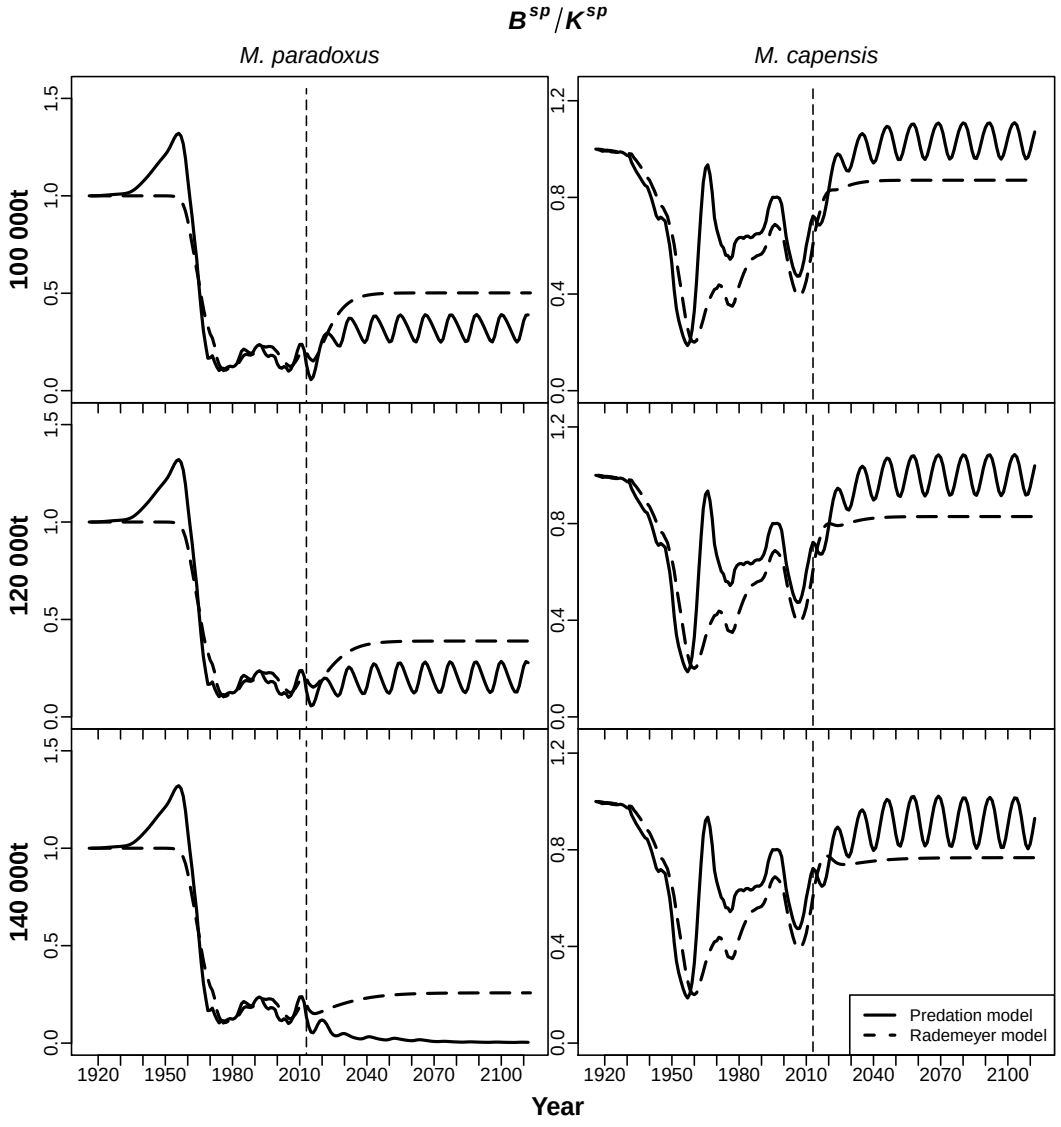


Figure 6.13: Projections under three levels of constant future catch. The projections were first calculated for the Rademeyer and Butterworth (2014b) model (courtesy of R. Rademeyer, *pers. comm.*), under the assumptions of constant proportional splits amongst fisheries, and constant fishing mortality ratios by species and gender (see Section 6.6 for further details). These catches were then used when projecting the predation model forward in time.

Chapter 7

Future work

This Chapter gives the details of possible future developments of and improvements to the hake model that merit further consideration.

Model simplification

As mentioned in the previous Chapter, one of the highest priorities is to simplify the current predation model in order to address the potential over-parameterisation of the predation formulation. The aim would be to develop the simplest formulation with the least number of estimable parameters that can take hake-on-hake predation and cannibalism into account in an explicit and biologically realistic manner, while still fitting the various types of data satisfactorily. First, the current equations would need to be evaluated to see if the number of estimable parameters could be reduced.

A starting point for this could be the formulation of the Holling Type II function feeding form in Equations 5.4 and 5.9, as these two Equations involve a total of 10 estimable parameters. There may be some confounding occurring between the parameters in the numerators and denominators, given the limited data available, so that this would seem the best place to begin the model-simplification process. A second aspect that could be simplified is the function for the θ^{s_p,a_p} (Equation 5.15), which determines the extent to which predation rates change with predator age. The current form incorporates two estimable parameters per species, and this might be reduce-able down to one parameter, and perhaps even the same θ^{a_p} function for both species, provided that this can be shown to maintain adequate flexibility for the predation dynamics.

There may also be elements of the underlying Rademeyer and Butterworth (2014b) model that could be simplified. It has already been shown that much simpler specifications for the longline selectivity are adequate in allowing the model to fit to the longline catch-at-length data satisfactorily, despite known changes in the fishing patterns of the longliners over the period for which they have operated. Of the 177 parameters estimated for the non-predation component of the model, over 100 are for the commercial and survey selectivities (see Table 4.7). While the Rademeyer and Butterworth (2014b) model may be capable of estimating the selectivities at such a level of detail, it would be worth investigating if these selectivities could be simplified for the predation model given the additional complexities with which it has to contend in the estimation of the predation mortality rates. One aspect that would need to be taken into consideration, however, is that the current predation model exhibits a poor fit to the *M. capensis* South Coast commercial offshore catch-at-length data and to the *M. paradoxus*

South Coast spring survey catch-at-length data. These fits would need to be improved, and simplifications to the selectivity functions could be justified only if good fits to the catch-at-length data are not compromised.

A draw-back to the manner in which the equations of the predation model have been parameterised to allow for the initial population set-up (see Section 5.3.5.1) is that the values for most of the estimable predation-related parameters (apart from those for the preference function) do not have direct biological interpretations. It could be useful if a parameterisation could be achieved that allows for more meaningful biological interpretations to be associated with the parameters.

The predation model in its current form requires about 24 hours to run and uses between 9 to 14 GB of RAM — this even after considerable time was devoted to improving the efficiency of the code by making use of matrix and vector algebra as much as possible. The reason that the model is so memory-intensive is primarily because of the monthly time step: instead of performing annual calculations for the 97 years from 1916 to 2013, the calculations have to be carried out for each of the 12 months of each year, i.e. well over 1000 time-steps. Once the parameter-simplification outlined above had been achieved, it would be worthwhile investigating whether coarser time intervals might still be able to provide acceptable results.

The data and the likelihood

Following a model simplification, the next aspect that would need to be investigated is alternative weightings for the various likelihood components. Although efforts have been made in this thesis to find objective bases for setting the variances (and hence the weightings) related to the different data types included in the negative log-likelihood, there is room to argue alternatives, and in particular different weightings for the ICSEAF CPUE, the catch-at-length and the diet data merit consideration. The panel for the 2015 International Stock Assessment Workshop recommended that the methods of Francis (2011) be implemented (with one iteration) to evaluate appropriate weights for the different likelihood components.

Regarding the diet data that are available to the predation model, there are several areas that would merit further investigation:

(i) The values assumed for the daily ration have a substantial impact on the model results. Further investigation of literature should be carried out, and new information as it becomes available in the literature should be monitored for further details on the values and trends with size/age for this quantity.

(ii) The methods of Andersen (2001), Andersen and Beyer (2008), Andersen (2012) and Andersen *et al.* (submitted), which relate gastric evacuation rate to the square root of the mass of the stomach contents, should be investigated to evaluate their ability to refine and improve the methods for calculating the proportion of hake in the diet of hake predators.

(iii) During the development of the predation model, an initial attempt was made to fit to the preference data by length directly by converting the age-dependent $\hat{\chi}_{say}^{s_p a_p}$ (the model-predicted proportion of hake prey of species s and age a consumed by predators of species s_p and age a_p in year y; see Section 5.4.2) to a length-dependent form $\hat{\chi}_{sly}^{s_p l_p}$. After all, preference is fundamentally driven by a length- (size-) related mechanism, and the coarse approach used in Section 5.4.2 to convert the length data to ages using a form of cohort-slicing to convert the preference data to an age-basis for fitting purposes might introduce bias. The first attempt made use of the age-length matrices $A^{s_p l_p a_p}$ and A_{sla} to convert the age-based to length-based preference functions. However the difficulty that immediately arose was that the use of the age-length

matrix for each of the predator and prey species introduced excessive variance in the resulting $\hat{\chi}_{sly}^{s_p lp}$ matrix, which the model countered by estimating unrealistically narrow predator-prey preference functions. An approach was developed that estimated the parameters of a predator-prey preference function by length, rather than age, and derived the associated age-dependent preference function from that. This operated in the same way that length-specific selectivity may be converted to an effective age-specific selectivity in circumstances where length-at-age distributions are assumed to be time invariant (see for example Equation 4.19). Initial implementation of this approach indicated that this indeed enabled fitting to preference data by length directly, with estimates of preference functions that were realistically broad in terms of the predator:prey length ratio, but the approach also resulted in instabilities in the overall estimation process, so that the more robust estimation approach of fitting to the preference data by age was kept in place. These issues of instability should be investigated in future work as the length-based formulation would seem the one to be preferred in principle.

(iv) Some thought should be given to the sampling strategies implemented by DAFF to collect the biological samples that inform the diet component of the predation model. This strategy (as described in Section 3.1.1.2) may well introduce biases in the diet data, since the target number of samples for each length group can be collected from any depth stratum. A better approach would be to set a target for each depth stratum. Furthermore, it would be beneficial to collect a greater number of samples for the larger hake, since a large proportion of the samples from these length groups have everted stomachs and are consequently unusable. Whether either of these suggestions could be implemented practically (especially given the relatively few larger hake that occur in the catch) would need to be evaluated by the scientists at DAFF.

(v) The panel for the 2015 International Stock Assessment Workshop recommended that the diet data should be developed by DAFF based on predator age rather than predator length, since most of the hake for which stomach content data are analysed have been aged. The use of the data in this form in the predation model would simplify the fitting process since the model is age-based.

(vi) The current predator model encounters estimation difficulties as a result of sparse data and confounding effects. An investigation should be conducted using the model to determine which further data that could be collected would hold the greatest potential to improve estimation performance.

Coastal segregation

The panel for the 2011 International Stock Assessment Workshop recommended that the predation model should ignore coastal structure and exclude the South Coast data initially, but should include coastal structure at a later point since hake are opportunistic feeders and their diets will reflect the abundance of the various prey types in their environment. On the South Coast, for example, *M. paradoxus* are much less abundant than on the West Coast, and as such will likely form a smaller component of the *M. capensis* diet. The current predation model assumes, however, that the diet data from the West Coast applies to the predation dynamics of the hake populations on the South as well as on the West Coast.

In order to implement a coastal split in the predation model, the first step required would be to analyse the diet data separately for each coast, which would include the full coast-specific analysis of the proportion of hake in the diet of hake predators. The incorporation of such a coastal split into the model could be challenging. The model would have to either keep track of separate components of each population on the West and the

South coasts, and estimate movement between the coasts (i.e. a movement model), or treat predation on the West Coast and South Coast on a basis similar to separate fishing fleets — i.e. the "areas-as-fleets" approach (recommendation A3 of Table 5.A.1). Given these complexities, it would be realistic to attempt a coastal split only once the base case predation model has been simplified.

Depth segregation

It is well established that the diets of hake predators change with depth. The hake predation model takes this into account implicitly through a simple depth-availability vector that allows the effective *M. capensis* preference to shift from *M. capensis* to *M. paradoxus* prey as the predators grow older. A more formal approach that models depth segregation explicitly is not likely to be feasible, given the added complexities and additional data required for such a stratification, as well as the increased computing time, although a two-depth stratification may be attempted. Alternatively, more sophisticated methods for modelling preference functions that change with predator age (as a proxy for depth) could be investigated as an "intermediate" approach. An investigation would need to be made into whether the relatively small sample sizes of the diet data would allow for reliable disaggregation by depth.

Seasonal segregation

A further aspect of the variability in the hake diet is a seasonal effect, as noted by Payne *et al.* (1987) when comparing the hake summer and winter diets. Since the predation model implements a monthly time-step, it would be fairly straight-forward to fit to different sets of diet data for the different seasons of the year. However, whether the existing diet data could support further segregation by season (given the already sparse data for particularly the older hake) without compromising estimation variance would have to be investigated.

Stock-recruitment relationship

The choice of the stock-recruitment relationship to use is one of the major uncertainties of the Rademeyer and Butterworth (2014b) assessment approach. Apart from the formulation of the relationship (either the Beverton-Holt or the modified Ricker form), there are further aspects relating to the stock-recruitment relationship that would need to be explored for the predation model.

(i) As has already been mentioned in Chapter 6, the customary interpretations related to the Beverton-Holt and modified Ricker stock-recruitment relationships (such as at what fraction of pristine abundance MSYL might be achieved) are based on the assumption that natural mortality is time-invariant. An exercise would need to be undertaken to investigate the relative shapes of the recruitment and mortality curves with biomass in order to ascertain whether the standard interpretations related to the stock-recruitment function parameters apply in the same way for the predation model. This is also important since such interpretations are often used to set bounds on parameters in the estimation process.

(ii) The implications of whether recruitment is taken to occur before or after predation should be explored, as per recommendation B4 of Table 5.A.1 (the model currently assumes recruitment to occur before predation).

(iii) The current predation model assumes that the recruitment occurs continuously throughout the year. Evidence suggests, however, that there are peak spawning seasons (see Durholtz *et al.* 2015). The

monthly time step in the predation model would allow for such peaks in the recruitment to be mimicked by the model. However, Durholtz *et al.* (2015) also point out that there seems to have been a shift in this within-year recruitment pattern over time, so that care needs to be taken that unintentional biases are not introduced if inappropriate assumptions for peak recruitment periods are made by the model.

(iv) Taking predation and cannibalism into account in the recruitment (e.g. Link *et al.* 2012) could be a simpler alternative approach to incorporating this effect into the mortality rates. However, such an approach assumes that cannibalism impacts mainly the youngest hake, whereas the results of this predation model suggest that hake up to age of 7 are subject to a notably higher mortality rate owing to predation and cannibalism. Nonetheless, it would be worth investigating such alternative approaches to ascertain their ability to represent the hake-on-hake predation and cannibalism dynamics, as was recommended by the panel for the 2014 International Stock Assessment Workshop.

Upgrade to level of the Rademeyer and Butterworth (2014b) model

To aid the initial development process of the predation model, certain simplifications were made to the Rademeyer and Butterworth (2014b) model. The first of these pertains to sex-disaggregation, which the predation model in its current form ignores. The predation model may, at some stage, need to be sex-disaggregated, although this task should likely be undertaken only once the base case predation model has been simplified. Such an extended model would have to make assumptions about the gender-split of the hake prey consumed by hake predators, but there would be no immediate way to verify the model-outputs for this gender-specific prey consumption, since prey items in stomach samples cannot be sexed given the current sampling protocols.

Secondly, the predation model does not fit directly to age-length-keys in order to estimate the growth curve parameters, as is done for the Rademeyer and Butterworth (2014b) model. It would be interesting to attempt to do this for the predation model, since the cohort structure of the hake population may be perceived differently in a predation and a non-predation model.

Model structure

Certain key aspects concerning the model structure that should receive further attention are listed below.

(i) The predation model implements only a Holling Type II functional form. Different forms should be explored (for example as was done by Kinzey and Punt 2009); alternative forms may produce better fits to the data. Particular note is taken of the option of a ratio-dependent functional response (S. Gaichas, *pers. comm.*; see for example Berryman 1992 and Gutierrez 1992). But even if the use of different forms does not produce better fits to the data, it could provide valuable insights into the predation dynamics of the hake population, particularly regarding the robustness of some of the key results of this thesis.

(ii) A competition effect was introduced to the predation model in a simple manner by bounding the total predation mortality rate P_{saym} (Equation 5.3) at a value of P_{lim}. This predation mortality rate is, however, summed across all predator species and ages, and as such the P_{lim} does not constrain the predation by individual predator cohorts. An alternative approach would be to limit the predator species- and age-specific predation rate $V_{saym}^{s_p a_p}$ (Equation 5.4). Competition could, however, also be taken into account explicitly through the implementation of a functional response form such as predator-inteference (as was done by Kinzey and Punt 2009, and earlier for Cape hake by Punt and Butterworth 1995), but it may prove

difficult to estimate the values of the competition-related parameters of such a form given the relatively sparse data available.

(iii) The assessments used in the development of OMP-2014 showed that the *M. paradoxus* depletion levels are particularly sensitive to assumptions about the pre-1977 split of the catch between the two hake species (Rademeyer 2012). In essence these assumptions pertains to the time assumed for the change-over from a *M. capensis* to a *M. paradoxus* dominated offshore trawl fishery. Sensitivity to this would need to be tested for the predation model.

(iv) Monitoring data collected for hake (e.g. size-composition data, stomach samples) are generally available by length, and since the model is age-based, age-length matrices are used to convert the age-based model outputs to length-based model outputs to enable comparison to the length-based data. These age-length matrices are assumed to be time-invariant, i.e. it has been assumed that the length structure within a given age cohort has not changed over time. However, given that the selectivity/preference of both the fishery and predators of hake are much more likely to be length-specific, the length structure within an age group will change with time. Ideally, the hake assessment models should track cohorts by age *and* length (as for example as for the GADGET model: www.hafro.is/gadget) to take full account of this, but the computational implications of such a structure are substantial, and not likely achievable with current computing power. Intermediate complexity models would, however, also be considered.

(v) The predation model makes the assumption that the hake populations were at stable (and oscillation-free) equilibrium before fishing commenced. Koen-Alonso and Yodzis (2005) found that cannibalism can influence this pre-exploitation equilibrium structure to the extent that a population may not be at (or close to) a stable equilibrium when exploitation starts. Such considerations could be investigated in the future, but would seem to be of a lower priority.

Other predators

Punt and Butterworth (1995) incorporated an "other predatory fish" component into their hake multi-species model (which also included seals), and found this inclusion to have a substantial impact on the model results. Those authors concluded that care needs to be taken to ensure that all major sources of predator-prey interactions are taken into account in a model if it is to qualify as a Minimal Realistic Model (MRM, Butterworth and Harwood 1991).

The panel for the 2011 International Stock Assessment workshop recommended that the predation model should ignore other predators initially, but should consider such effects at a later stage. A major (non-hake) predator of hake is the Cape fur seal (roughly 40% of the seals' diet is hake; see Punt *et al.* 1995). A simple approach to taking seal predation into account would be to incorporate an additional term in the hake mortality rate that is proportional to the seal population abundance estimates (for each year). The incorporation of an "other predatory fish" component could also be considered using a similar approach to Punt and Butterworth (1995) (see Section 2.3.1.4). Including other predators (and thus developing a genuine Minimal Realistic Model) has a high priority if the hake multi-species model is to provide a substantial improvement to the single-species models the underlie the present provision of management advice.

Projections under future catch

Section 6.6 presents the results of the projection of the base case predation model into the future. The method used to obtain these results was a very simple, first-cut approach and should be refined for future work. As discussed in Chapter 6, alternative approaches would be to project under the assumption of constant fishing mortality rates or to apply the hake Management Procedure (MP) to the predation model (the predation model then also providing an important robustness test in selecting amongst alternative candidate MPs).

Once the predation model might have been developed to a satisfactory level (i.e. the over-parameterisation addressed and key further developments such as coastal segregation incorporated), an important exercise would be to generate sets of future pseudo-data for various plausible variants of the predation model, in order to better assess what are the key uncertainties of the model and their implications for the potential future status of the hake resource under various management scenarios.

Chapter 8

Summary of findings

A brief summary of the main findings and conclusions of this thesis is provided here.

- The hake predation model is able to take hake-on-hake predation and cannibalism into account explicitly, while still providing a reasonable fit to the various sources of data available (related to abundance catch-at-size and feeding information). There are, however, some indications of data conflicts as well as of potential model over-paramterisation, which need to be addressed.
- When cannibalism and predation are taken into account, the *M. paradoxus* population exhibits a predation release in first half of the 20th century in response to a reduction of the *M. capensis* predator population by the early fishery. The *M. paradoxus* population peaks in 1956 at a spawning biomass that is some 30% larger than the pre-exploitation biomass. The *M. capensis* population shows an increase in the 1960s that is not evident to the same extent in the non-predation models, suggesting that the *M. capensis* population also experienced a predation release as a result of the exploitation of *M. capensis* predators by the fishery (and consequently reduced levels of *M. capensis* cannibalism).
- Despite these predation releases, the predation model estimates similar, even slightly higher, extents of depletion for *M. paradoxus*. The chief reason for this is the requirement to reflect the large drop in the ICSEAF CPUE data from the mid-1950s to mid-1970s. Higher predation levels give greater predation release, but show stronger oscillatory behaviour which is then unable to also fully reflect the ICSEAF CPUE decline. This finding is contrary to the hope expressed by some stakeholders in the fishery that taking account of this predation release would result in estimates of a substantially less depleted *M. paradoxus* resource.
- Direct estimates of the daily ration of Cape hake are not available since gastric evacuation studies have not been conducted for this species. Bounds for biologically realistic daily rations were obtained from the literature and from theoretical considerations of fish bioenergetics. Without any constraints on the daily ration, the predation model does not provide biologically realistic estimates for these rations. With constraints on daily ration in place, the model remains able to provide a reasonable fit to feeding and other data sources, but also exhibits a tendency to "switch" between fitting one data source closely to fitting another. This is particularly the case for a higher *M. paradoxus* daily ration which results in a worse fit to the historical ICSEAF CPUE data.

- While the predation model still needs to be developed further, it shows good potential as a tool to improve the assessment and management of what is South Africa's most valuable fishery. An immediate and important spin-off from this work is the explicit provision of an indication of appropriate values to choose for hake mortality-at-age vectors. Choices for these vectors constitute a major uncertainty in the current (non-predation) assessments of the hake resource, and these predation model results could provide a more justifiable basis for these vectors.

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